

CHAPTER 1

General Introduction

A successful pig production has to consider all economically important aspects of producing pork. Besides efficient lean meat growth the reproductive performance of the sow and marketing aspects of pork are of increasing importance. Successful marketing of pork requires the quality of pork to be of high standard. Historically, reproductive performance and meat quality characteristics were not considered as feasible breeding objectives due to low heritabilities, difficulty of measurement and lack of economic importance (McPhee, 1982). Decline in pork quality and lack of improvement in reproductive traits suggests that these areas require greater consideration (Ollivier et al. 1990).

Meat quality has become a major concern in pig production. In Australia, genetic improvement for meat quality has so far only been achieved by selection against stress susceptibility using the halothane test. Studies in Europe showed that in the absence of the halothane gene meat quality characteristics still have a genetic variation of 20 % which could be used in breeding programs (de Vries et al., 1994b). Meat quality can be described through a range of characteristics but the meat quality deficiency, which is of most concern to the consumer, is pale, soft and exudative meat (PSE) (Jeremiah et al., 1994). Its significance to the Australian pork industry was shown by a PRDC survey (PRDC, 1993). The genetic variability of these traits and their genetic relationships with carcass and production traits is unknown for Australian pigs.

Improvement of reproductive performance in the sow focuses mostly on selection for litter size. However, genetic improvement obtained in number of piglets weaned has mainly been achieved by an increase in number of litters per sow rather than a greater litter size (de Vries and Kanis, 1993). Possible explanations might be unfavourable genetic correlations with production traits (Webb, 1991) and leanness (Johansson and Kennedy, 1983; Cleveland et al., 1988). In addition, increase in litter size appears to be associated with decrease in piglet birth

weight and survival (Haley et al., 1988). However, average piglet weight at birth needs to be considered as a separate trait due to its favourable relationship with piglet mortality (Rydhmer et al., 1992). At present, evaluation programs evaluate litter size in single trait analyses assuming no genetic associations with other traits. To genetically improve reproductive performance of the sow, additional reproductive traits have to be analysed and their genetic relationships with other reproduction and production traits have to be studied.

The objective of this thesis is to estimate genetic parameters for growth rate and feed conversion ratio as well as carcass, meat quality and manufacturing traits for Australian pigs. To achieve this objective a data set is accumulated including production, carcass, meat quality and manufacturing traits. This data set is then linked to reproductive performance of sows to estimate genetic relationships between reproduction traits and to obtain estimates of genetic correlations with production, carcass and meat quality traits. This information will provide a basis for establishing a breeding program that incorporates all economically important traits.

A literature review of systematic effects is presented in chapter two. Systematic effects are summarized for efficient lean meat growth, meat quality traits and reproductive performance. Reviewed systematic effects influencing lean meat growth are preweaning effects as well as effects of feeding regime and housing systems. The review of systematic effects for meat quality traits focuses on the influence of the halothane gene on meat quality traits but also summarizes environmental influences on the slaughter procedure including lairage time and differences in transport, stunning and chilling. The summary of genetic parameters includes only recent studies for the main traits since other reviews included previous studies. Firstly, a review of heritability estimates is given and secondly, a summary of genetic correlations between traits is presented. Special emphasis is given to the influence of feeding regime and housing systems on estimates of genetic correlations. Estimates of genetic correlations between reproduction traits and other performance traits are sparse and therefore results from selection experiments are presented as further information.

Chapter three gives information about the material used in this study and includes a description of the enterprise responsible for data recording. Background information consists of climatic data, feeding regime during the project and housing system as well as a description of slaughter procedures. Next, the testing and recording procedures are described along with information about the structure of the data set. Recorded traits and systematic effects influencing these

traits are discussed. The last part gives an overview of the data set obtained from the herd recording system of the enterprise which includes the reproductive performance of sows.

Methods and models used for analysis are described in chapter four. Firstly, an overview of the development of variance components estimation is given. Secondly, theoretical background information about restricted maximum likelihood procedures is presented. Special emphasis is placed on derivative free procedures and algorithms using average information. The development of the appropriate model for each trait includes analysis of fixed effects as well as random effects which are analysed by applying a log likelihood ratio test.

Chapter five summarizes results from variance components estimation. The first part presents univariate results for each group of traits. Heritability estimates are presented for Large White and Landrace pigs separately and differences between the two breeds are discussed. In addition, the influence of the data structure on simultaneous estimation of additive genetic effects and litter effects is studied. The second part presents genetic, environmental and phenotypic correlations between traits. Estimates of genetic parameters are discussed in relation to the feeding regime and testing procedure. Possible influences of the halothane gene on estimates for meat quality traits are investigated along with the influence of the processing procedure on estimates of genetic correlations between manufacturing traits and carcass and meat quality traits.

In the final chapter, aspects of this project including testing procedures and measurement techniques are discussed. Estimates of genetic correlations obtained from bivariate analyses are compared with multivariate estimates. Analysed traits are discussed and implications of results are studied, which involves implementing various selection indices incorporating different options.

CHAPTER 2

2. Literature review

The phenotypic performance of an animal is influenced by the genotype of the animal as well as the environment the animal lives in. Therefore, in order to estimate heritabilities and genetic correlations, genetic and environmental influences on the performance of an animal have to be distinguished. Additive genetic links between animals are taken into account through the numerator relationship matrix in an animal model while environmental influences are included in the model as fixed effects. Possible environmental influences consist of differences in management practices, including feeding and housing systems, and for reproductive performance possibly differences in mating systems. Another influence originates from differences in season or differences in slaughter procedures for meat quality traits. The analysis of these fixed effects is not only needed for genetic evaluation but also provides a basis for evaluation of the management system. This information might then be useful in order to compare heritabilities and genetic correlations across studies.

This chapter consists of two parts. Firstly, an overview of possible environmental influences on lean meat growth, meat quality and reproductive performance is given. Secondly, heritabilities and genetic correlations are summarized for production, carcass and meat quality traits as well as reproductive traits of the sow.

2.1 Summary of systematic effects

2.1.1 Systematic effects for feed efficiency, lean tissue growth and carcass traits

Overall performance of pigs in lean growth rate and carcass characteristics is dependent on various factors. These were summarized by Bereskin (1990) for feed efficiency as one performance characteristic, but they also influence other growth and carcass traits. Nutritional

quality of the feed influences growth and carcass performance through different levels of protein, energy and availability of critical amino acids, minerals, vitamins and feed additives. Management practices can affect pig performance. These management practices can include feed wastage from self-feeders, feeding regimes eg. restricted versus ad libitum feeding regimes, and housing systems. Additionally, environmental conditions affect tested pigs through differences in temperature, humidity and odours. Finally, lean growth rate, feed efficiency and carcass characteristics might also be influenced by preweaning factors eg. litter size as well as the genotype and sex of the animal. A summary of the influence of these factors on production and carcass traits is given in this chapter.

2.1.1.1 Preweaning

Muscle fibre number and muscle fibre size determine muscle mass with muscle fibre number probably being the most important factor (Miller et al., 1975). A comparison between different strains of pigs showed that fast-growing pigs have more muscle fibres than slower growing pigs (Miller et al., 1975). Dwyer et al. (1993) analysed Landrace pigs from seven litters finding no correlation between average daily gain and fibre number from birth to 25 kg of live weight. However, a significant correlation between average daily gain and muscle fibre number, as well as a significant correlation between feed efficiency and muscle fibre number, was found for the growth period from 25 to 80 kg liveweight.

Prenatal development of muscle fibres and factors influencing their development were reviewed by Stickland (1994). Muscle fibres consist of two distinct types, primary myofibres and secondary myofibres. Primary myofibres are formed during the initial stages of myoblast fusion and build the framework for the formation of larger populations of smaller secondary myofibres. In the pig, only primary fibres are present at 38 days of gestation and their number gradually increases until the 60th day of gestation. Secondary fibres are formed between 54 and 90 days of gestation.

In a study containing 48 Large White pigs, Dwyer and Stickland (1991) found that differences in primary fibre number were responsible for most of the variation in total muscle fibre number between litters. Within litters, variation in fibre number was determined by both primary number and secondary to primary fibre number ratio. However, when only the extreme pigs of each litter were compared, variation in fibre number was only due to differences in secondary to primary fibre number ratio, confirming results from Handel and Stickland (1987). It was therefore suggested that the number of primary fibres is determined by the genotype of the animal, whereas secondary fibre number is influenced by uterine environmental factors. Dwyer

et al. (1994) investigated the effect of doubling feed intake during three periods of gestation, 25 to 50 days, 50 to 80 days and 25 to 80 days, on muscle fibre number and on later growth and efficiency of growth. An increase in nutrition did not affect the number of primary muscle fibres significantly and therefore the total number of muscle fibres was also not significantly changed. However, a higher level of nutrition increased the secondary to primary fibre number ratio and subsequently increased growth rate and gain to feed ratio from day 70 to slaughter by 10% and 8%, respectively.

These physiological mechanisms suggest possible effects of litter size and parity number on growth performance. Standal (1973b) found a significant influence of litter size and parity on growth rate, backfat and liveweight at test. However, each effect accounted in all cases for less than 1% of the total variation and it was concluded that these effects are of minor practical importance. There was a tendency that pigs from gilt litters and especially large gilt litters grew slower than average. Litter size seemed not important for second litter sows, while pigs from large litters in later parities showed a reduced growth rate.

In contrast to Standal (1973b), Willeke and Richter (1979) found no significant effect of parity on growth rate and backfat while litter size was only significant for growth rate. Average daily gain was reduced for the first parity with the second parity showing the highest average daily gain and a continued decline of growth rate for later parities. Backfat increased by 1.85 mm from the 1st to 6th parity. The effect of litter size was manifested through a continuous decrease in growth rate once litter size exceeded 12 piglets.

2.1.1.2 Nutrition

Growth rate of a pig is dependent on intake of both energy and protein. Several studies have focused on protein and lipid deposition rate in relation to energy intake when protein intake was not limited. Linear-plateau relationships between energy intake and protein accretion were first proposed by Whittemore and Fawcett (1976) and later experimentally demonstrated over a 45 to 90 kg body weight range by Campbell et al. (1985) and Dunkin et al. (1986). This linear plateau relationship is shown in Figure 2-1. The slope of the linear-plateau relationship was influenced by the sex and genotype of the animal (Campbell and Taverner, 1988). It was steeper for boars in comparison to gilts and barrows and steeper for leaner genotypes which lead to a higher plateau of maximum protein deposition. The effect of body weight on the linear relationship parameters has been widely discussed. Whittemore (1986) suggested that the slope between energy intake and protein deposition is largely unaffected by liveweight. However, Quiniou et al. (1995) found that the slope decreased with increasing body weight

confirming Dunkin et al. (1984) and Dunkin and Black (1985). In their studies, the potential rate of protein accretion increased with live weight up to 70 to 80 kg, after which it began to fall.

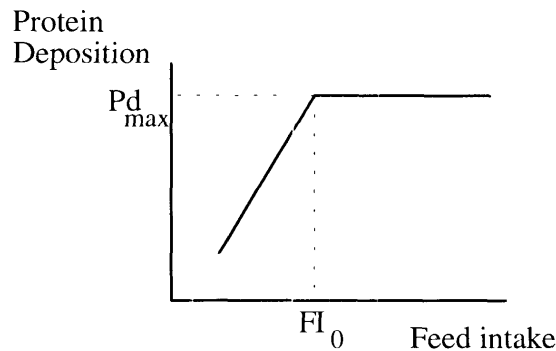


Figure 2-1 Linear-plateau relationship between protein deposition and food intake. (FI_0 is the minimum food intake to realize maximum protein deposition (Pd_{max}))

The effect of energy intake on performance showed a linear increase in average daily gain with increased energy intake (Campbell et al., 1985; Quiniou et al., 1995). Food conversion ratio was not affected by energy level (Quiniou et al., 1995), although Campbell et al. (1985) found a higher feed conversion ratio for a feed intake above 33 MJ DE per day and per pig. Other studies analysed the effect of protein intake at a given energy level of the feed (Campbell et al. 1984). There was a significant interaction between the effects of dietary protein content and feeding level for growth rate, food conversion ratio and protein deposition. On both energy levels, growth rate, feed efficiency and protein deposition improved until a certain level of dietary protein (164g/kg crude protein). A further increase in crude protein had no effect on growth performance characteristics and protein deposition for the lower energy level whereas growth rate, feed efficiency and protein deposition deteriorated with increasing crude protein content for the high energy level diet. These results suggest that protein deposition in pigs, given diets adequate in protein, was a function of energy intake and independent of protein intake.

Stern et al. (1995) studied the existence of genotype by protein level interaction for growth rate and lean meat percentage. Two selection lines of pigs were selected for high lean tissue growth rate over four generations on either a high (HP) or a low (LP) dietary protein level. Growth rate was significantly higher for the LP-line when protein levels were low, but no differences between the lines were found under a moderate to high protein level. Lean percentage showed no differences between the two lines at any level of protein.

Influences of dietary factors on feed intake were reviewed by Henry (1985) concluding that voluntary feed intake in the growing pig is primarily dependent on energy concentration. The growing pig tends to adjust its voluntary feed intake in such a way that it maintains its energy requirements. However, voluntary feed intake is limited progressively by gastrointestinal capacity of the pig and therefore level of energy intake slightly declines as energy concentration in the diet decreases. Additionally, voluntary food intake is modulated by changes in the protein : energy ratio. A marginal deficiency in protein supply induces a compensatory increase in feed intake to meet existing requirements, with the side effect of a higher carcass fatness.

2.1.1.3 Feeding regime

A comparison between restricted and ad libitum feeding showed an increase in feed intake and daily weight gain of 20% for ad libitum feeding (Thomke et al., 1995a,b). Meat percentage was lowered by around 1.5% for ad libitum feeding when compared with restricted feeding. Fat accretion was thus increased for ad libitum feeding and was deposited as fatty tissue as well as intramuscular fat. A reduction of crude protein of 10% below the recommended level lowered growth performance and lean meat percentage.

Cameron and Curran (1995) investigated genotype by feeding regime interaction by testing pigs from selection lines under ad libitum and restricted feeding regimes. Selection under a restricted feeding regime was mainly beneficial for response in growth rate whereas backfat did not exhibit differences between the two feeding regimes. It was therefore suggested that a genotype by feeding regime interaction exists for growth rate but not for backfat. These findings are in agreement with earlier results from Bereskin et al. (1990) and Kanis (1990a).

2.1.1.4 Housing

Pigs are sent to test stations at a later stage of their life and the question arises whether environmental effects before station testing should be considered when evaluating the test results. The correlation between average daily gain before and within test station was low (Rydhmer et al., 1989). An explanation for this low relationship could be different housing systems for on-farm testing and for test stations.

Nielsen et al. (1995) studied the effect of group size on feed intake patterns and growth performance. Pigs kept in larger groups made fewer but longer visits to the feeder and ate more and faster per visit than pigs kept in the smaller groups. However, no differences were

found between group sizes in total daily feed intake, daily liveweight and feed conversion ratio which agrees with results from Hunt et al. (1985) (cited in Nielsen et al., 1995). A rank index based on pairwise aggressive interactions was not correlated with any of the production or feeding behaviour variables (Nielsen et al., 1995).

Pigs housed in groups ate faster, had a higher food intake per meal but fewer meals per day, less eating time per day and a lower daily food intake than pigs penned individually (de Haer and Merks, 1992). Individually housed pigs have been found to have an improved production in terms of a higher growth rate and a reduced backfat (de Haer and de Vries, 1993a) compared to group housed pigs. However, de Haer and de Vries (1993a) did not find differences in daily feed intake and feed efficiency between individual and group housed pigs and the improved growth may have been due to other factors such as feed intake patterns. In individual housing higher digestibility coefficients were correlated with more short visits per day, fewer large meals and an optimum rate of feed intake. In both housing systems better digestibility coefficients were correlated with a higher growth rate and an improved feed conversion. Foster et al. (1983) reported that with few but large meals per day pigs spent less energy on food intake behaviour and were energetically more efficient.

McBride et al. (1964) showed that social position has an effect on the growth of pigs fed ad libitum from 8 to 16 weeks of age. However, Hansen et al. (1982) found only an effect of social rank on average daily gain when only one feeder was available for each pen. This is in agreement with results from Vargas Vargas et al. (1987) who found that feeding behaviour, aggression and social rank were associated with average daily gain in time-restricted systems. The more aggressive pigs visited feeders more frequently, displacing pen mates from feeders and gaining weight faster. In ad libitum systems these differences were not found, confirming results from Hansen et al. (1982). Meese and Ewbank (1973) concluded that when several pigs were able to eat at the same time, eating activity and weight gain are independent of ranking order.

2.1.1.5 Sex

Campbell et al. (1985) demonstrated that because of their higher capacity for lean tissue growth, entire male animals will exhibit faster and leaner growth at all levels of energy intake than females or castrated males. Males therefore contain less fat and more protein and water in the empty body than females (Campbell et al., 1985). Furthermore, it was shown that entire males have a lower feed conversion ratio than females. These findings are in agreement with de Haer and de Vries (1993b) who noted a significant sex effects in an ad libitum feeding

system, with boars having a higher growth rate and a lower feed efficiency. Campbell (1988) suggested that because males have a higher tissue requirement of protein and amino acids entire males are also more sensitive to dietary protein deficiency than gilts or barrows.

Castrates showed a nine percent higher feed intake and a 11% higher daily weight gain in comparison to females under ad libitum feeding. Feed efficiency was not different for the two sexes in this feeding regime (Thomke et al., 1995a,b). Additionally, a feeding regimen by sex interaction was indicated through lower carcass meat percentage on ad libitum feeding in relation to restricted feeding for castrated males than for females.

2.1.1.6 Season and temperature

An early Norwegian study indicated that the effect of season on growth rate and backfat is of minor importance (Standal, 1973a). There was no consistent effect of season in two years on growth rate, although there appeared to be a tendency for pigs born in the summer months from June to September to have less backfat. When the interaction year-season was fitted it explained 1.28% of the variation for backfat and 0.1 to 0.2% of the variation in growth rate. Seasonal influences are of higher magnitude in Australian production systems as was shown in a study incorporating one Dutch and two Australian data sets (de Vries et al., 1994a). The model included season defined in two month steps and sex of the animal and explained 21.1, 42.2 and 39.8 percent of the variation for Dutch Yorkshire, Australian Large White and Australian Landrace, respectively. The higher proportion of variation explained by the model for average daily gain in the two Australian breeds was mainly due to high seasonal influences. This high seasonal influence might be explained by differences in temperatures between seasons as was shown in a Japanese study (Sakai et al., 1992). Fastest growth rates were noted in the temperature range between 16 and 20°C whereas slowest growth rates were recorded at temperatures of 8°C or lower and 24°C or higher. Average daily gain was reduced by approximately 150 grams for the extreme temperature classes in comparison to the adjacent temperature class.

2.1.1.7 Various systematic effects

Christian et al. (1980) studied differences between barrows and gilts for various carcass characteristics. In comparison to gilts, barrows had a lower percentage of ham and loin, smaller loin area, shorter carcasses, more backfat and increased marbling. Differences in carcass characteristics were also found between different genotypes. Lean crossbred pigs exhibited lower marbling and colour scores, less backfat, longer carcasses, larger loin eye area

and higher ham and loin percentages. Comparison between different slaughter weights showed a reduction in ham and loin percentages, an increase in loin eye area and an increase in carcass length, backfat and dressing percentage.

Comparing carcass and wholesale cuts between barrows and gilts, Langlois and Minvielle (1989) found no differences between barrows and gilts for hot carcass weight, loin weight and shoulder weight. However, ham weight was significantly larger for females. In addition, the importance of breed effects on carcass weights was studied. In comparison to Hampshire, Duroc and Yorkshire sired pigs, offspring from Landrace boars had significantly lower ham, loin and shoulder weights whereas no significant differences existed between the other breeds.

2.1.1.8 Genotype

Growth performance and body composition varies for different genotypes of pigs (Campbell and Taverner, 1988). Pigs selected for growth rate (strain A) showed higher growth rate, lower feed conversion ratio and higher protein content than pigs that had not undergone selection. Additionally, there was a line by level of energy intake interaction for growth rate. Pigs selected for high growth rate had a greater increase in growth rate with increasing feeding level than pigs that had not undergone selection. There was no intrinsic factor for protein deposition for pigs from the high growth line showing an increase in protein deposition up to the level of ad libitum feeding. In contrast feed efficiency and protein deposition deteriorated for pigs that had not undergone selection after they reached their optimum with a medium energy level.

In an Australian study, McPhee et al. (1981) compared growth performance of Large White and Landrace pigs. Large White pigs exhibited a higher growth rate, higher feed intakes and a better feed efficiency.

Growth and carcass performance of Dutch Landrace and Great Yorkshire pigs were compared by de Haer and de Vries (1993b). Great Yorkshire had a higher growth rate, lower backfat and higher lean percentage at equal levels of daily feed intake. Great Yorkshire pigs were therefore more feed efficient. Additionally, daily feed intake of this breed was distributed over many, relatively small meals in comparison to Dutch Landrace pigs.

Mrode and Kennedy (1993) showed breed differences in growth and carcass characteristics for Canadian Yorkshire, Landrace and Duroc pigs. Duroc pigs exhibited the fastest growth rate

whereas Landrace pigs had the highest feed intake and the poorest food conversion ratio. Yorkshire pigs were the leanest breed.

Genotype effects on daily feed intake were shown by Kalm (1986). Comparing daily feed intake of Pietrain and Landrace pigs showed that the daily feed intake of Pietrain pigs was roughly 87% of the daily feed intake of Landrace pigs. This difference might partly be due to a higher incidence of the halothane gene which appears to lower daily feed intake for homozygote carriers (Webb and Simpson, 1986).

A New Zealand study (Smith and Pearson, 1986) compared voluntary feed intake, growth performance, carcass composition, and meat quality of Large White, Landrace and Duroc pigs. No differences between breeds were found for growth rate, but Landrace pigs had a higher feed conversion ratio, due to a higher voluntary feed intake. Additionally, Landrace pigs showed a lower lean meat percentage than Duroc and Large White pigs, which were similar in this characteristic.

2.1.2 Systematic and genetic effects for meat quality traits

Quality is defined differently by different people. A detailed description of the term “quality” was given by Hofmann (1994) who distinguished between quality in the meaning of “goodness” and in the meaning of “condition” of a product. Hofmann (1994) concluded that the more comprehensive meaning of quality is “condition” while good quality in the meaning of goodness is only a special case - a particularly positively evaluated condition. This leads to the definition of the properties and characteristics of a product which can be objectively measured. Pork quality is defined as the sum of product quality and production quality (Hofmann, 1986). Product quality consists of four groups of quality characteristics that describe the properties of meat as a product, whereas production quality includes factors such as genetics, housing, feeding, transport and slaughter of pigs.

Product quality can be described by considering sensory, technical, nutritional and hygienic factors (Hofmann, 1986). Sensory factors are meat characteristics such as colour, taste and juiciness that influence the decision of the consumer to buy pork. Technological factors are of more importance to the processing industry since preparation, packing and suitability for processing into various products are dependent on these factors. Important characteristics of this group are drip loss, pH-value and tenderness. Nutritional factors concern chemical composition and nutritional aspects of pork. The lean meat content and fat content of a carcass

and their composition are important characteristics in this group. In this context, it should be mentioned that the lean meat yield is sometimes regarded as a meat quality trait even when it is basically a quantity trait. The fourth group of characteristics includes the hygienic status of meat which gives information about residues, contaminants and the shelf life of meat.

Production factors affecting meat quality consist of the genetics of the animal, housing, and feeding during the growing period, including the use of antibiotics and growth promotants. Other issues are the treatment of animals during transport, stunning and bleeding. Handling of carcasses during scalding and dehairing may also influence meat quality. In the future, animal welfare issues might be of concern and these factors will have to be addressed by both the pig producing and processing industries.

2.1.2.1 Pork quality deficiencies - pale soft and exudative meat and dark firm and dry meat.

The now commonly used term PSE meat, indicating pale, soft and exudative meat was first introduced by Briskey (1964). PSE meat is mainly found in pigs that have been selected for rapid and efficient growth, leanness and carcass conformation. These types of animals show the porcine stress syndrome more frequently, which is characterized by muscle tremor, an increased respiratory rate, systemic acidosis and a rise in body temperature (Lister, 1987). This can cause death of affected animals in situations of stress and is therefore of importance to the producer, but also leads to PSE meat. A characteristic of PSE meat is rapid glycolysis, which leads to a high lactic acid concentration in the muscle before and shortly after slaughter. This causes a rapid pH decline after slaughter which, in conjunction with high temperature, results in the denaturation of muscle proteins and membrane leakage, which induces a pale appearance and high drip loss (Bendall and Wismer-Pedersen, 1962; Warris and Lister, 1982).

Dark, firm and dry (DFD) meat is induced in animals that have been subjected to exhaustive exercise or prolonged stress before slaughter, leading to a glycogen deficiency within the muscle (Bouton et al., 1971). The amount of lactic acid produced by glycolysis depends on the amount of available glycogen, so the final pH of DFD meat remains high (Hamm, 1960). This causes physical characteristics such as dark colour and high water holding capacity. An additional undesired property of DFD meat is its sticky surface which contributes to low shelf life causing problems in marketing DFD meat. Threshold values of different meat quality characteristics for classification of PSE and DFD meat are listed in Table 2-1.

Table 2-1 Threshold values for different meat quality characteristics used to classify PSE and DFD meat (Warner et al., 1993; O'Shea pers. comm. 1996)

Characteristic	PSE - meat	DFD - meat
pH at 45 minutes p.m.	< 6.0	
pH at 24 hours p.m.		> 6.2
colour (L-value)	> 55	< 47
drip loss percentage	> 4.0	< 0.5

2.1.2.2 Halothane gene

Hall et al. (1966) found similarities between the porcine stress syndrome and malignant hyperthermia. The halothane gene as it became commonly known is also called malignant hyperthermia syndrome (MHS) gene. Its effect on stress susceptibility and meat quality is closely related to muscle morphology which was briefly summarized by Schmitten (1993) (Figure 2-2). The effects of the halothane gene are due to a cytosin-thymin-transition which induces a change in the amino acid sequence of the Ca^{2+} -release-channel-membrane protein (the Ryanodin-receptor protein). As a consequence, the limit of releasing Ca^{2+} from the sacroplasmic reticulum (SR) in stress situations is considerably reduced for stress susceptible pigs (Knudson et al., 1990). In the situation of an insufficient energy supply (ATP) through intracellular anaerobic glycogenolysis, the energy dependent back stream of Ca^{2+} from the atkin-myosin complex is inhibited. In this context muscle morphology plays a major role. Although the Ryanodin-receptor gene is genetically influenced through the halothane gene in all muscle types, negative influences on meat quality occur mainly in muscles with a higher muscle mass. There is therefore a close connection between muscle structure and muscle hypertrophy with regard to stress susceptibility and meat quality.

Muscle hypertrophy is closely related to large muscle diameters which is mainly due to an increase in glycolytic muscle fibre type IIB. Muscle fibres are classified into two classes, muscle fibre type I and muscle fibre type II consisting of type IIA, IIB and IIC (Essen-Gustavsson, 1993). Muscle fibre types differ between muscles with the *m. longissimus dorsi* having a large proportion of type IIB fibres (80 to 90%) (Essen-Gustavsson et al., 1992; Karlson et al., 1994), while *m. vastus intermedius* has a large proportion of type I fibres (70 to 80%) (Essen-Gustavsson, 1993). Important for meat quality, glycogenolysis occurs to a greater extent in fibre type IIB than in type I and IIA fibres.

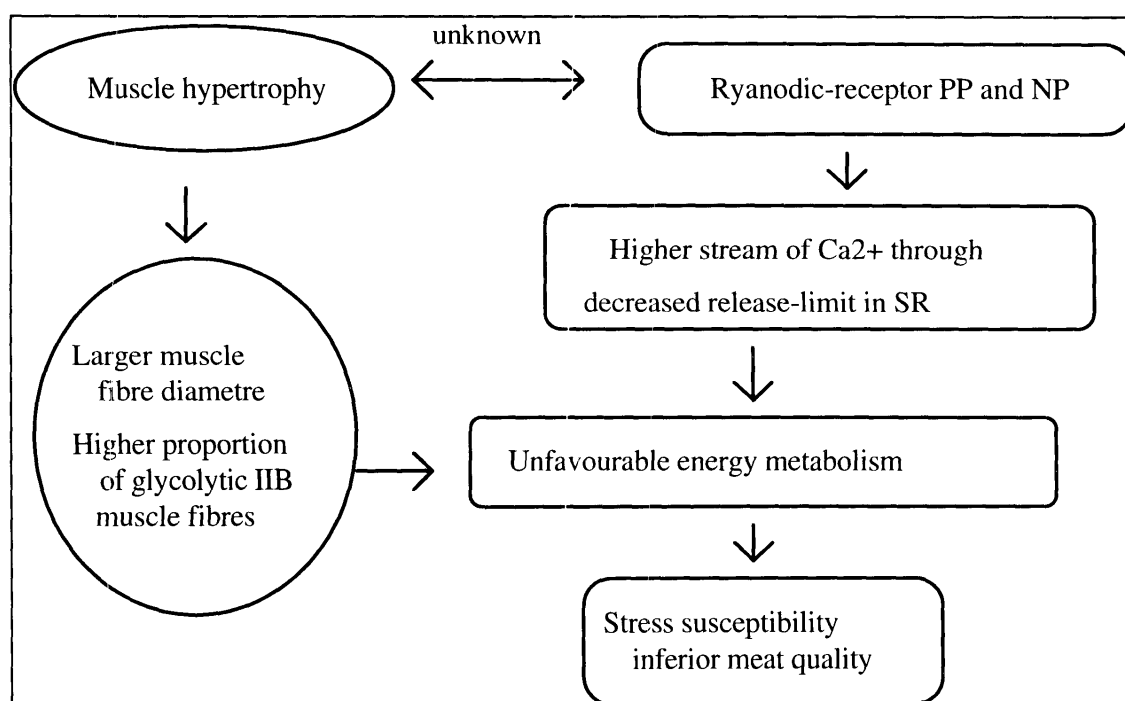


Figure 2-2 Relationships between effects of MHS-gene (PP, NP) and muscle hypertrophy (Schmitt, 1993)

The effect of the halothane gene on glycogen depletion of different muscle fibres was studied by Essen-Gustavsson et al. (1992). Pigs carrying two copies of the halothane gene had a significantly increased fibre diameter for all three fibre types and a lower capillarization of the muscle. Glycogen depletion was significantly increased in muscle fibre type IIA and IIB. In this scenario, the proportion of depleted type IIB fibres is negatively correlated with pH at exsanguination, and positively with drip loss and reflectance values (Lundström et al., 1989). No differences were found in ultimate pH between genotypes. However, the only carcass with a high ultimate pH in the *m. longissimus dorsi* muscle was obtained from a halothane positive pig. It was therefore concluded that although DFD can be obtained from all pigs in the case of long-term stress, the mild pre-slaughter handling of pigs in the described study suggests the DFD pigs should be regarded as stress susceptible (Lundström et al., 1989).

A somewhat different relationship between depleted muscle fibres and meat quality was found by Karlsson et al. (1994) who studied a population of halothane free pigs. The proportion of depleted type IIB fibres in *m. longissimus dorsi* was positively correlated with ultimate pH and pH at exsanguination, and negatively with drip loss and reflectance values. When 30% or more of IIB type fibres were depleted of glycogen, the muscles showed a tendency to become DFD, as the meat had high ultimate pH, high water-holding capacity and low reflectance value. It

was suggested that the glycogen depletion pattern of more than 30% was caused by adrenalin induced stress resulting from physical activity, with varying proportions in individual animals. This could be due to the inclusion of entire males and gilts in this study in contrast to the study undertaken by Essen-Gustavsson et al. (1992) which used castrates and gilts. It is well known that males show an aggressive behaviour at lairage (Lundström et al., 1987) possibly explaining the differences between the studies by Karlsson et al. (1994) and Essen-Gustavsson et al. (1992).

Since Fujii et al. (1991) and Otsu et al. (1991) developed a gene probe to distinguish between the three halothane genotypes it has been possible to analyse the performance of the three genotypes. Growth and carcass performances as well as meat quality characteristics are summarized in Table 2-2 for the three genotypes. Two German studies by Wittmann et al. (1993) and Peschke et al. (1993) showed a superior growth rate for heterozygous pigs (Nn), followed by homozygous carriers (nn). An Australian selection study, with selection placed on low backfat and high growth rate, found different performance levels for the three genotypes (McPhee et al., 1994). Pigs not carrying the halothane gene (NN) or just one copy of the gene (Nn) had a superior growth rate than homozygous carriers in the control line which had undergone no selection. For the selection line homozygous non-carriers showed a superior performance over homozygous carriers as well as over heterozygotes. Homozygous carriers had the highest lean meat percentage which was equivalent to the lowest backfat depth, as shown by MCPhee et al. (1994), with heterozygotes having an intermediate performance in carcass characteristics. With respect to meat quality traits, the halothane gene had a detrimental effect. All studies found a low pH at 45 minutes for homozygous carriers, with the mean being below 6.0 and therefore exhibiting PSE meat. Heterozygotes were intermediate in pH value at 45 minutes relative to the homozygous genotypes.

Different levels of PSE and DFD meat for the two lines in the selection study by MCPhee et al. (1994) indicate that other genes responsible for leanness and the halothane gene have a different influence on meat quality. The halothane gene was associated with PSE, while other genes responsible for an increased leanness led to a higher incidence of DFD meat (McPhee and Trout, 1995). The high incidence of DFD meat for pigs from the selected line not carrying the halothane gene could be due to the long-term transport stress before slaughter. Under these conditions the mortality rate for homozygous carriers was higher (13%) in comparison to halothane heterozygotes, with a mortality rate of 2.6%, and homozygous non carriers, with a mortality rate of 1.4% (McPhee et al., 1994).

Table 2-2 Growth, carcass and meat quality traits for halothane genotypes

Study and trait	N	Breed	NN	Nn	nn
Average daily gain (gr.)					
Wittmann et al. (1993)	229	German Landrace	802	836	810
Peschke et al. (1993)	323	Pietrain	662	728	710
McPhee et al. (1994)	136	control line	550	550	530
McPhee et al. (1994)	94	selected line	630	600	520
Lean meat percentage (%)					
Simpson and Webb (1989)	214	British Landrace	57.1	59.8	60.6
de Smet et al. (1992)	949	Belgian Landrace*		60.9	61.7
Wittmann et al. (1993)	229	German Landrace	53.1	53.9	60.2
Schmitten (1993)	335	7 hybrid origin	56.8	58.7	60.2
Peschke et al. (1993)	323	Pietrain	62.6	64.5	65.2
Backfat depth (mm)					
McPhee et al. (1994)	136	control line	14.0	13.0	12.3
McPhee et al. (1994)	94	selected line	19.4	18.6	18.0
pH at 45 minutes p.m.					
Wittmann et al. (1993)	229	German Landrace	6.43	6.18	5.64
Schmitten (1993)	335	7 hybrid origin	6.55	6.20	5.66
Peschke et al. (1993)	323	Pietrain	6.52	5.94	5.54
McPhee and Trout (1995)	123	control line	6.40	6.23	5.96
McPhee and Trout (1995)	77	selected line	6.56	6.29	
Luxford (1995)		Large White	5.70	5.66	
Luxford (1995)		Landrace	5.75	6.09	
Colour (L-value)					
McPhee and Trout (1995)	123	control line	45.4	45.9	47.9
McPhee and Trout (1995)	77	selected line	42.4	44.7	
Luxford (1995)		Large White	52	55	
Luxford (1995)		Landrace	53	55	
Drip loss percentage (%)					
McPhee and Trout (1995)	123	control line	3.62	3.76	2.73
McPhee and Trout (1995)	77	selected line	2.28	3.62	
Luxford (1995)		Large White	1.35	2.18	
Luxford (1995)		Landrace	1.57	1.90	
PSE incidence (%)					
McPhee and Trout (1995)	123	control line	14.6	23.9	33.6
McPhee and Trout (1995)	77	selected line	8.3	18.3	
DFD incidence (%)					
McPhee and Trout (1995)	123	control line	19.8	29.2	27.7
McPhee and Trout (1995)	77	selected line	60.6	37.4	

* including Belgian Landrace crosses with Pietrain or German Landrace

2.1.2.3 RN gene

A new meat quality measurement was developed by Naveau et al. (1985), the so called “Napole” technological yield, which is a measure of cooked weight to fresh weight. Naveau (1986) postulated the hypothesis that a major gene called the Rendement Napole (RN) gene is segregating in two French lines which was supported by Le Roy et al. (1990) using segregation analysis. The unfavourable RN gene is completely dominant and an allele frequency of 0.6 was estimated for both lines. It increases the glycogen content of glycolytic muscles by about 70% (Estrade et al., 1993). This distinction was used by Lundström et al. (1996) to analyse the effect of the RN gene on meat quality. The RN gene has a detrimental effect on the capacity of the muscle to retain water, whether fresh or processed. Drip loss and cooking loss were therefore increased by 21% and 12% respectively, while the Napole yield decreased by 7%. It was suggested that these detrimental effects are a result of an increase in glycogen and a decrease in protein content, together with a lower ultimate pH value. At the moment there is no technique available to classify animals into three genotypes for the RN gene by using genetic markers, but research concerning the molecular background of the RN gene has begun in France (Milan et al., 1996), Sweden (Mariani et al., 1995) and in Germany (Rudat et al., 1995), locating the RN gene on chromosome 15 in swine.

2.1.2.4 Breed

Sellier (1988) compared ultimate pH and colour for three breeds commonly used in France: Large White, Pietrain and Belgian Landrace. With regard to these measurements, Large White pigs showed best results, with Belgian Landrace being intermediate and Pietrain having poorest meat quality. These differences were analysed with respect to the halothane gene and it was concluded that they are closely related to the frequency of this gene in these breeds. Pietrain had the highest level of pigs being sensitive to the halothane test whereas in the Large White population no pigs reacted to the halothane test.

Durocs are known for their higher intramuscular fat content, as demonstrated by Sellier (1988), who summarized intramuscular fat contents for various breeds from different studies. The average intramuscular fat content for Duroc pigs from two Swedish and one Swiss study was 3.9%, which was higher than the Hampshire breed average of 2.0% and well above the intramuscular fat content of Large White, Landrace, Pietrain and Belgian Landrace breeds ranging from 1.40% to 1.62%.

Meat quality characteristics of Duroc pigs have been compared with other breeds in various studies (McGloughlin et al., 1988; Cameron et al., 1990; Edwards et al., 1992; Ollivier et al., 1993). In these studies differences in meat quality characteristics between Duroc pigs and other breeds have been characterized controversially. Cameron et al. (1990) compared meat quality and eating quality of Duroc pigs and British Landrace pigs. Duroc *m. longissimus dorsi* was darker in colour, had a more intense red colour and contained more fat and less moisture than Landrace muscle. The taste and consumer panels scored Duroc meat as being more juicy, but less tender, having poorer flavour and being less acceptable than Landrace. It was suggested that the higher juiciness scores of Duroc meat were probably due to higher intramuscular fat content compared to Landrace meat. A Spanish study compared Duroc pigs with Pietrain and Belgian Landrace pigs, also finding that Duroc pigs had a darker colour and a higher ultimate pH (Ollivier et al., 1993). These results were not confirmed by Edwards et al. (1992) who found no significant differences between Duroc sired pigs and pigs sired by British Large White boars in either muscle reflectance values, pH measurements or in an assessment of eating quality characteristics by a trained taste panel. An Irish study (McGloughlin et al., 1988) compared Duroc sired pigs with Irish Large White and Irish Landrace pigs. No meat quality problems were observed in this trial but Duroc sired pigs had slightly paler meat, which was judged to have more flavour.

One explanation of these differences between studies might be, that Duroc pigs have been assessed by comparison with various breeds or crosses. Furthermore, there may be variation between the samples of Duroc included in the investigations, and therefore, some variation in the reported relative merit of the Durocs is to be expected (McGloughlin et al., 1988). This hypothesis is strengthened by the different levels of intramuscular fat content found in different studies. Although Duroc pigs always showed a higher intramuscular fat content than the corresponding comparison, intramuscular fat content differed between studies substantially with values ranging from 1.6% (Cameron et al., 1990) to 2.9% (McGloughlin et al., 1988; Ollivier et al., 1993).

Hampshire boars are used in breeding programs in France (Le Roy et al., 1990) or as terminal sires in a three-way cross in Sweden (Lundström et al. 1996). In comparison with other breeds, pork from Hampshire pigs is characterized by a lower ultimate pH in connection with the highest cooking loss (Monin, 1985), a higher water content, a lower protein content (Fjelkner-Modig and Tornberg, 1986; Wassmuth et al., 1991), and a higher glycogen content (Monin, 1985). Monin (1985) suggested denoting meat as “Hampshire type” meat when its qualitative deficiency results from an abnormally lowered ultimate pH which might be due to the dominant RN gene (Lundström et al., 1996).

2.1.2.5 Sex

Meat quality characteristics including water holding capacity, colour and pH were analysed for gilts and castrated males, finding no differences between the two sexes in these traits (Monin, 1985). However, significant genotype by sex interactions were found with Hampshire females having inferior meat quality than Large White females, whereas no breed differences were found for castrates.

Karlsson et al. (1994) compared meat quality characteristics and fibre type characteristics between entire males and gilts. Males had significantly smaller muscle fibre areas for type I, IIA and IIB fibres, compared with gilts. Among the meat quality traits males had a higher reflectance value than gilts whereas other meat quality traits including drip loss, and pH measurement exhibited no significant differences between the two sexes. The paler meat for entire males in comparison to gilts is in contrast to studies from Lundström et al. (1987) and Warris and Brown (1985) who found no differences in colour between entire males and gilts.

2.1.2.6 Nutrition

Comparing pigs selected for increased lean tissue growth rate on a high protein diet (18.5% crude protein) and a low protein diet (13% crude protein) Karlsson et al. (1993) found that pigs fed the high protein diet had a lower intramuscular fat content, higher shear force value, higher protein extractability, lower light reflectance, and a somewhat higher water holding capacity. However, these differences were not significant in the fourth generation of selection. Besides fibre volume, which was increased for pigs fed on the high protein diet, no other fibre type characteristic was significantly influenced by level of protein fed to these pigs (Karlsson et al, 1994).

2.1.2.7 Production system

Production systems seem to have no effect on pork quality as Warris et al. (1983) and van der Wal (1991) found no improvement in pork colour or waterholding capacity in pigs from free-range versus intensive production systems. Additionally, Jones et al. (1994) compared pH, shear value, soluble protein, colour and structure of meat from pigs fed indoors versus pigs fed outdoors, finding no differences in these characteristics between treatments.

2.1.2.8 Lairage time

Meat quality characteristics and carcass yield are affected by varying the time of feed withdrawal before slaughter (Tarrant, 1992). Jones et al. (1985) studied the effect of no fasting, 24 and 48 hours fasting with water restrictions in lairage, after pigs had already been withdrawn from food for 17 hours. Although ultimate pH was increased for longer fasting periods it did not lead to DFD meat. Additionally, drip loss percentage was reduced with increased lairage time. Despite these positive effects of prolonged fasting before slaughter, Jones et al. (1985) suggested to minimize fasting before slaughter, as prolonged fasting decreased liveweight and carcass yield. Fasting for 48 hours reduced liveweight by 6.8 kg with 75% of this loss being attributed to carcass yield loss. For a fasting period of 24 hours liveweight loss amounted to 3.75 kg and carcass yield loss accounted for 80% of this loss (3 kg). These findings are in agreement with Warris and Brown (1983) who found a liveweight loss of 0.21% per hour and a carcass weight loss of 0.11% per hour for the fasting period between 18 and 48 hours.

The effect of different duration of feed withdrawal prior to slaughter was analysed by Murray et al. (1989) for three lines of pigs with different genotypes with respect to stress susceptibility. Homozygous carriers of the halothane gene showed a high incidence of pale and exudative meat which was reduced from 57% at 0 hours of feed withdrawal to 9% at 48 hours of feed withdrawal. Feed withdrawal of 48 hours reduced the incidence of soft and exudative meat from 87% to 48%. The incidence of meat quality deficiencies was below 5% for halothane free animals and feed withdrawal had no effect on meat quality for these pigs. Heterozygote animals exhibited an intermediate pork quality, which was also improved with increasing lairage time. Murray et al. (1989) suggested that manipulation of feed withdrawal before slaughter might be a potential management practice to improve meat quality.

Eikelenboom et al. (1991) compared no fasting time with fasting periods of 16 and 24 hours followed by an interval of four to five hours for delivery and slaughter. Feeding until delivery resulted in a significantly lower pH at 45 minutes post mortem in the *m. longissimus dorsi*. Prolonged fasting for 24 hours led to a darker colour and decreased drip loss, whereas fasting for 16 hours did not reduce drip loss but colour was improved. A disadvantage of prolonged fasting is a higher incidence of DFD meat and Eikelenboom et al. (1991) concluded that a fasting period between 16 and 24 hours should be recommended to reduce PSE meat while minimizing losses in carcass yield. In contrast to the findings of Jones et al. (1985) and Eikelenboom (1991), Fernandez et al. (1992) in a study incorporating a (Landrace - Large White) - Hampshire three way cross, found no effect of lairage time on muscle glycogen and

ultimate pH after lairage for 2 or 24 hours. This suggests that there might be an interaction between genotype and handling in regard to ultimate pH. Finally, Tarrant (1992) concluded in a review that a lairage time of 12 to 18 hours would be the optimum to guarantee all above mentioned advantages and at the same time have only a minimum loss in carcass yield.

2.1.2.9 Transport, stocking density and mixing of slaughter animals

Transport of pigs starts in the fattening pen and van Putten (1982) gave guidelines how additional stress to the animals could be avoided by considering some basic principles on farm. These include for instance well-functioning doors, no troughs in doorways, no uneven floors and light areas to where pigs are moved. To reduce stress during transport and loading, rough treatment and the usage of electro goads should be avoided. Loading and unloading is preferably done with hydraulic lifts, and it is important that the slope of the loading dock is not too steep (< 20%) (Smulders and van Laack, 1992).

Stocking density on the truck influences body temperature, heart rate and respiratory rate especially in connection with high temperature and high humidity (von Mickwitz, 1982). In addition, Guise and Penny (1989a) found an increase in skin damage which implies poorer welfare, the incidence of rectal prolapse, and a lighter colour for pigs transported with a high stocking density (0.3m²/pig). Von Mickwitz (1982) proposed a loading density for slaughter pigs of 0.5m²/100 kg live weight which is now required for “certified pork” in Germany (Honikel, 1992), and suggested a 15% increase in space in hot and humid weather conditions. Dutch studies (Lambooy et al., 1985; Lambooy and Engel, 1991) recommended a stocking density for pigs of about 235 kg/m² as a reasonable compromise between animal welfare, cost of transport and meat quality. These studies compared stocking densities of 186, 232 and 278 kg/m². Both studies found that the high stocking density did not allow all pigs to lie down at the same time, which induced a continuous alternation of lying down and standing up. At the lower stocking density of 186 kg/m² all pigs lay down earlier after the start of the transport and the proportion of pigs that remained lying during transport was higher (Lambooy and Engel, 1991). At the stocking density of 232 kg/m² all pigs had just enough space to lie down. However, it took a longer time until all pigs lay down. In addition, the effect of ventilation on pig behaviour and meat quality was examined. High temperatures observed in compartments during international journeys have a negative influence on animal welfare (Lambooy, 1988), which might be partly overcome by artificial ventilation. Ventilation or showering during transport did not affect the activities of pigs nor did they influence their behaviour (Lambooy and Engel, 1991). Meat quality characteristics were only influenced to a low extent by ventilation.

A high stocking density can also result in a higher incidence of fighting. The effect of this fighting on meat quality was analysed by Warris and Brown (1985) who found a higher ultimate pH, which is associated with DFD meat, with the *m. semimembranosus* and *m. adductor* showing the greatest damage. In addition, a high damage score was associated with higher corticoid, lactate and glucose levels in the blood. No significant relationship was found between damage scores and pH measured at 45 minutes after slaughter, reflectance value or drip loss of the *m. longissimus dorsi*. There was a tendency for boars to show more carcass damage caused by fighting (Warris and Brown, 1985).

A higher incidence of fighting can occur when pigs are mixed during rearing, transport or in lairage. Mixing pigs at either loading or unloading, or at both points, had no significant effect on meat colour in *m. longissimus dorsi* at 20 hours post mortem, but it had a significant effect on the frequency of skin blemish values (Guise and Penny, 1989b). Karlsson and Lundström (1992) compared meat quality characteristics of pigs kept as a unit from fattening to slaughter and of pigs that were mixed at the start of the fattening period, at transport to the slaughterhouse, at lairage and at slaughter. The study included barrows and gilts, and a higher incidence of PSE (19.1% versus 13.0%) and of DFD (7.0% versus 4.0%) was found for the mixed group in comparison to the unmixed group. Classification of pigs into meat quality classes was based on pH measurements. The different level of PSE and DFD pigs for the two treatments reflects differences in pH measurements with pigs kept in one group having a higher pH at 45 minutes and a lower ultimate pH. There was no significant difference in meat colour between the two treatments.

2.1.2.10 Stunning

The method used for stunning must result in immediate induction of unconsciousness to reduce stress for the animal. Nevertheless all stunning methods even when applied in the right way produce stress to the animal (Troeger and Woltersdorf, 1991). This will lead to an increase in catecholamines and lactate in the blood and will affect metabolism and lower pork quality.

The question, which stunning method should be used, has been discussed extensively (Eikelenboom, 1983). Objections against electrical stunning are that this procedure results in more haemorrhages and broken bones. Major objections against CO₂ stunning are that the time lapse between the administration of CO₂ gas and full unconsciousness is too long (15 to 40 sec.). Comparing different stunning methods under practical conditions, Garrido et al. (1994) found no significant differences between electrical and CO₂ stunning on meat quality characteristics.

The stunning procedure should not exceed a few seconds and a time lapse as short as possible should be allowed between stunning and sticking to improve meat quality. In a review, van der Wal et al. (1978) concluded that electro-shock stunning with 300 volts, with short stunning times and minimal lapse of time between stunning and sticking, will result in better pork quality. Anil (1991) compared the time until a pig regains consciousness after electrical stunning to determine the voltages required for stunning. In contrast to van der Wal et al. (1978), it was concluded that a voltage of 150 volts should be used for 3 seconds in connection with a maximum stunning to exsanguination interval of 15 seconds to ensure pigs do not regain consciousness following the stun. No advantages could be found by increasing the voltage to 300 volts. These findings were supported by results from Troeger and Woltersdorf (1990) who found that higher voltages increase the incidence of PSE meat.

Over the last few years CO₂ stunning equipment has been installed more frequently although the capital costs and running costs are quite considerable (110 to 300 grams CO₂/pig) (Troeger and Woltersdorf, 1991). Troeger and Woltersdorf (1991) analysed the optimum gas concentration and gas exposure time in relation to animal welfare and meat quality. They concluded that the CO₂ concentration of the stunning gas should be 80 to 90% depending on the exposure time. Short periods of exposure to the gas (90 sec.) require high CO₂ concentration (90%) and vice-versa.

New developments in stunning techniques include electrical stunning by direct brain stimulation (Lambooy, 1994) and the use of high pressure waterjet in combination with electro-immobilization (Lambooy and Schatzmann, 1994). Lambooy (1994) concluded that 25 volts is sufficient for effective stunning of slaughter pigs when electrodes are in direct contact with the brain. This is not always the case in practical conditions and therefore a voltage of 90 volts was recommended. Additionally, Lambooy and Schatzmann (1994) investigated the use of high pressure waterjets that are used for cutting and drilling in solid material for stunning slaughter pigs. Although it appears to be a humane and suitable method to stun pigs in a slaughterhouse, it has the disadvantage of convulsions immediately after stunning. To overcome this problem, the stunning method is combined with an immobilizing electric current. This has an unfavourable effect on meat quality and it was suggested that alternative restraining methods should be tested to overcome problems in meat quality.

2.1.2.11 Chilling

Honikel (1987) found that rapid chilling of fast glycolysing muscles reduces the rapidly occurring drip loss and reduces the paleness of meat. The effect of rapid chilling and showering

of pigs before slaughter was investigated by Long and Tarrant (1990). Rapid chilling at -20°C for 3 hours without an air blast lowered evaporative chill losses in sides of pork by 27 to 29% compared to normal chilling. Additionally, pH fall in loin and leg muscles and drip loss in intact pork legs was reduced by rapid chilling. Combining rapid chilling with showering of pigs with cold water before slaughter was more effective than either treatment alone in regard to rate of pH fall and internal light scattering in the *m. longissimus dorsi*. The possible disadvantage of fast chilling, cold shortening, was not observed in this study. Advantages of rapid chilling were confirmed by Garrido et al. (1994). Meat quality was improved by rapid chilling, as denaturation of protein decreases and therefore water holding capacity increases. However, a recent study (van der Wal et al., 1995) found no significant effect of chilling regime on meat quality except for variables related to tenderness. The Warner-Bratzler shear forces were higher after extreme rapid chilling (-30°C) in connection with high air velocity (4m/s) indicating an increased risk of cold shortening as sarcomere lengths were reduced. The effect of temperature on sarcomere length was studied by Honikel et al. (1986). At a temperature of 10°C the minimum shortening was measured. A higher degree of shortening of up to 50% was recorded above and below this temperature.

Taylor and Martoccia (1995) studied the effect of low and high voltage electrical stimulation on meat quality to overcome problems in tenderness after rapid chilling. The most tender meat was produced by high voltage electrical stimulation (700 volts, 90sec.) applied 20 minutes post-slaughter, followed by rapid chilling. The improvement in tenderness was achieved with no detrimental effect on either drip loss or colour.

2.1.3 Systematic effects for reproductive traits of the sow

Reproductive performance of the sow is influenced by various factors which were divided into two categories by Clark and Leman (1986). The first category includes parity, age at first conception of first litter, number of matings per conception, season, previous lactation length and previous weaning to conception interval. These effects are often recorded in commercial piggeries and are available for analysis. The second category includes husbandry practices, nutrition and disease. These effects are often not recorded but might influence reproductive performance of the sow. The above factors influence all reproductive traits of the sow, whereas the number of piglets after transfer and the age of the litter at weighing are only of importance for the 21 day litter weight.

2.1.3.1 Age at first conception and parity

The reproductive capability of the gilt begins with attainment of puberty. Hughes (1982) reviewed factors affecting the attainment of puberty and concluded that chronological age of the gilt is a better measure of physiological age and reproductive development than weight. The effect of chronological age on litter size was reviewed by Clark and Leman (1986) finding an increase in litter size as chronological age increases.

In a review about the effect of parity on litter size, Clark and Leman (1986) concluded that litter size is smallest in the first parity, reaches maximum size in parities three, four and five and remains nearly constant or slowly declines as parities increase. They further concluded that factors which influence litter size should be investigated within parity to avoid confounding effects of parity on these factors. Later studies found a steady increase in litter size from first parity to fifth parity (Rodriguez et al., 1994). For Iberian pigs, which are a low fecundity breed, litter size increases monotonically even after parity eight (Perez-Enciso and Gianola, 1992).

Walker and Young (1993) found that milk yield in gilts is 20% lower than in multiparous sows, possibly as a consequence of lower feed intake and the need to meet body-tissue growth. Sows in parities three to six had superior performance in litter traits resulting in about 4 kg more litter weight at 21 days (Yen et. al., 1987). In contrast, 21 day litter weight and piglet weight at 21 days was greatest in the second litter and decreased afterwards in studies analysing data from an experimental farm (Rydhmer, 1992) and data including Iberian pigs (Rodriguez et al., 1994).

2.1.3.2 Season

In Wild Boar an anoestrous period occurs during summer and autumn months (Mauget, 1982). Although complete cessation of oestrus activity due to season is not common in the domestic pig, seasonal variation in reproduction performance exists. Seasonal infertility is reported to have a variety of manifestations: delayed puberty in gilts, prolonged weaning to oestrus interval, higher incidence of embryonic loss and abortions and therefore a failure of mated sows to farrow, as well as a reduction in litter size. The most important aspect of seasonal infertility is the reduction in the proportion of mated sows that farrow (Love et al., 1993). The effects of season on reproductive performance can be divided into the effects of photoperiod and temperature.

In Australia, high temperatures are reached during summer months and their effect on sow reproductive performance was investigated by Paterson et al. (1978). The number of sows returning to service after mating increased to 19.7% when the mean daily temperature exceeded 32°C in comparison to 12.7% for matings in other temperature ranges. It was concluded that heat stress around the time of mating may affect ovarian function, resulting in temporary infertility and an endocrine imbalance. However, Hennessy and Williamson (1984) showed for an Australian piggery that the symptoms of the so called 'summer or seasonal infertility' can be manifest at any time of the year when the appropriate combination and intensity of stressful stimuli is given. The effect of heat stress on sow lactation was studied by Black et al. (1993). They concluded that there is a direct effect of high ambient temperature on milk production of sows and that lactating animals have special mechanisms for reducing milk output when suffering from heat exposure.

An US study analysed a data set with 38000 litters finding that month and year explained less than one percent of the total variation for nine different reproductive traits (Strang, 1970). These traits included number of pigs born alive and litter weight at three weeks. The herd effect accounted for five to seven percent of the variation for most traits and explained 15% of the variation for litter weight at three weeks.

In contrast, farrowing season showed a clear effect on litter size and on survival rate up to three weeks in the study by Dabao et al. (1983). Litters born in winter were larger than in any other season of the year, but their survival rate was the smallest one at 21 days. Season also affected 21 day litter weight. No cross-fostering was practised resulting in the highest 21 day litter weight during the summer months. These findings are in agreement with earlier studies showing a strongly negative effect of low temperature on piglet survival and development (Blecha and Kelly, 1981; le Dividich, 1981) demonstrating their poor thermo-regulation and their relatively high critical temperature.

2.1.3.3 Nutrition

Delay or onset of breeding season between October and January in Wild Boar is related to the level of mast production in the forest. Therefore it seems likely that nutritional factors may influence the timing of reproduction in the Wild Boar (Mauget, 1982). King and Williams (1984) studied the effect of different feeding regimes during lactation and weaning to conception interval on sow reproductive performance. Ovulation rate and subsequent litter size, as well as piglet mortality, were not affected by feeding level during lactation. However, a higher feed level between weaning and conception did positively influence ovulation rate and

litter size of the subsequent litter. In a later study, King (1986) found an effect of feed intake during lactation on piglet growth with higher feed intake leading to higher piglet growth prior to weaning. Much of this effect was expressed during the last week of lactation. Comparing older and younger animals it was shown that the more mature animals were better able to withstand the effects of food restriction during lactation. The importance of body reserves for first litter sows was demonstrated by Mullan and Williams (1989) showing that they can be used by the sow to buffer nutritional stress induced by a low food intake during lactation. Average piglet weight at 21 days was not affected by feed intake levels but sows with a low feed intake showed a greater backfat loss than sows fed at a high level. This suggests that these sows effectively mobilized body fat stores to support an adequate level of milk production (Johnston et al., 1986).

2.1.3.4 Litter size

The effect of the size of the litter in which a gilt was raised on production and reproduction characteristics of primiparous sows was studied by van der Steen (1985a). A significant influence of litter size was found for weight at weaning with piglets coming from smaller litters having a higher weaning weight. No significant effect of litter size on backfat thickness and age at first oestrus was found. The effect of litter size on gilt's own performance has been shown to be negative with gilts coming from a small litter producing larger litters than gilts raised in bigger litters (Nelson and Robison, 1976; Rutledge, 1980; van der Steen, 1985a). In a further study, van der Steen (1985b) concluded that the negative influence of maternal effects on litter size is mainly environmental and can be eliminated by standardizing of litter size after birth at a fixed level for those litters from which gilts are going to be selected. A later study (Gu et al., 1989) found no effect of litter size on the reproductive performance of the sow when cross-fostering was practised. Furthermore, Rydhner et al. (1989) showed that a large fraternity size does not necessarily have an unfavourable influence on the litter of the gilt if heavy piglets are chosen for replacement.

2.1.3.5 Maternal effects

There is an ongoing discussion whether maternal effects have a negative influence on litter size. Using a stochastic approach, Roehe and Kennedy (1993) studied the influence of maternal effects on the accuracy of evaluation of litter size. Maternal effects influence response to direct selection, even when the magnitude of maternal effects is low. Additionally, ignoring maternal effects leads to biased environmental and genetic trends. It was concluded that maternal effects should be included in the model of genetic analysis. However, the estimation of maternal

effects requires separation of direct and maternal effects which can only be achieved in large data sets with complete pedigrees.

A negative covariance between direct and maternal performance was indicated by earlier studies (Revelle and Robison, 1973; Nelson and Robison, 1976) and also found in a later study by Vangen (1980b). Maternal effects seemed to be increased for number of piglets alive at 21 and 42 days.

In an experimental breeding herd, Jørgensen (1989) investigated the influence of maternal effects on litter size. Heritabilities for litter size were obtained through a dam - daughter regression and a maternal granddam-granddaughter regression. Estimates of heritabilities were lower for dam-daughter regression than for maternal granddam-granddaughter regression. This decrease in estimates of heritabilities is due to a negative covariance between maternal and direct genetic effects which influence the coefficients from the dam-daughter regression.

It was shown by Southwood and Kennedy (1990) that for a Landrace population heritabilities for number of piglets born alive in the first parity were underestimated when maternal effects were not included in the model. The correlation between direct heritability and maternal heritability was strongly negative with a value of -0.92. However, no significant maternal effects were found by Mercer and Crump (1990) and by Perez-Enciso and Gianola (1992) for an Iberian population on litter size in nucleus lines. In a recent study, Roehe and Kennedy (1995) found no maternal effects in a Landrace population for litter size, but suggested an influence of maternal effects on moderate genetic correlations between litter size in the first and second parity in Yorkshire.

2.1.3.6 Service sire

The service sire could influence the reproductive performance of the sow by either semen quality and quantity or by genetic effects that influence embryo development and survival. The effect of service sire on number of piglets born alive has been analysed widely (Strang, 1970; Mabry et al., 1988; Buytels and Long, 1991; See et al., 1992). This effect explained 0.3% (Strang, 1970) to 3% (Marby et al., 1988) of the total variation for number born alive.

2.1.3.7 Number of piglets weighed

With increasing number of pigs after transfer from three to 13 piglets, adjusted 21 day litter weight increases linearly. Every added piglet resulted in a 3.0 kg increase in 21 day litter

weight (Yen et al., 1987). In an experimental data set, Rydhmer (1992) found a decrease of individual piglet weight at weaning (6 weeks) of 0.3 for each extra pig. The effect of number of piglets weighed on 21 day litter weight was recently analysed by Tholen et al. (1996b) in an Australian study. Number of piglets weighed was fitted as a linear and quadratic covariable. Estimates were 8.48 kg, 9.35 kg and 7.82 kg for the linear covariable and -0.13 kg, -0.16 kg and -0.06 kg for the quadratic covariable for the first to third parity respectively. This indicates quite substantial differences in weight gain per additional piglet between herds which might be due to differences in number of piglets per litter and might be influenced by the lactation length.

2.1.3.8 Weaning to conception interval and lactation length

Fahmy et al. (1979) reported an increase in litter size as the weaning to conception interval increases. More recent studies found a reduced litter size for a weaning to conception interval of seven to ten days (Leman, 1990) or a weaning to conception interval of 9 to 12 days with an increase in litter size with increasing weaning to conception interval thereafter.

Clark and Leman (1984, cited in Clark and Leman, 1986) have shown a 0.1 pig per day reduction in litter size for each 1 day decrease in lactation length below 28 days. This was only found in females that conceived within 10 days of weaning. No association between lactation length and subsequent litter size was found in females that conceived more than 10 days after weaning. Thus the effects of lactation length on litter size are likely to be influenced by weaning to conception interval. In addition, Tholen et al. (1996a) showed the dependence of weaning to conception interval on lactation length. Both short (< 20 days) and long (> 29 days) lactation periods led to an increase in weaning to conception interval by two to three days relative to the optimum of 21 to 23 days. A method that describes the joint effects of lactation length and weaning to conception interval more clearly is the farrowing to conceiving interval (Clark and Leman, 1986).

2.1.4 Conclusions

This first part of the literature review summarized systematic effects for important performance traits. It was discussed how preweaning factors might influence growth performance. In this respect, information about the development of primary and secondary muscle fibres during gestation was given. Nutrition was described as another major factor influencing growth performance. The effect of restrictions in protein and energy intake on growth performance

was discussed and it was shown that energy intake and protein deposition have a linear-plateau relationship to protein deposition which is influenced by the sex and the genotype of the animal. Another source of variation originates from differences in housing systems which might become important when on farm performance and test station performance have to be compared.

The effect of systematic effects on meat quality traits were looked at in regard to PSE and DFD meat. The influence of the halothane gene on meat quality and its interaction with muscle hypertrophy was discussed. It was shown that breed differences in meat quality traits are based on a different level of the halothane gene and arise from different levels of intramuscular fat content which is increased in Duroc pigs. Optimal meat quality is dependent on a good slaughter environment. This includes lairage time, handling of animals during transport and stocking densities as well as slaughter procedures with stunning and chilling techniques being of greatest importance. The influence of these factors on meat quality was discussed.

The review of systematic effects on reproductive performance of the sow was based on factors that are recorded under practical situations. These include age at first parity and the effect of parity which have to be seen in the context of the maturity of the animal. The effect of season might originate from an anoestrus in Wild Boar and is of special significance in Australia due to high temperatures during summer months causing heat stress. It was shown that the unfavourable effect of large litter size on reproductive performance can be overcome by standardizing litter size. Subsequently, different results from various studies about the influence of maternal effects on reproductive performance of the sow were summarized. Finally, results from more recent studies analysing the effect of number of piglets reared on litter weight traits were shown. Regression coefficients for this effect varied considerably across herds which might be due to differences in other management practices. These might include differences in piglets per litter and variation in lactation length and weaning to conception interval.

2.2 Summary of genetic parameters

2.2.1 General introduction of traits

The starting point for a breeding program is a proper definition of a breeding objective, as it determines testing schemes to be applied and the direction of genetic change of the population. A false definition of the breeding objective has negative consequences for animal production. Usually the breeding objective includes growth rate, lean meat content and feed conversion ratio to describe efficient lean meat growth. The reproductive performance of the sow is mostly described through litter size or number of piglets weaned. Selection criteria are traits that are actually measured on the animal and mostly comprise average daily gain, backfat thickness and litter size. To stay competitive future breeding programs will have to look at further traits. Possible further traits that are of importance are briefly discussed in this section.

The antagonistic effect of selection for reduced backfat on feed intake has been shown by Brandt (1987) for three breeds in Germany. Taking genetic parameters and economic values of the traits studied into account, Cameron (1992) predicted 20 to 35% additional gains, when individual feed intake is added to the selection index. A continuing reduction of feed intake may limit further improvement in lean growth rate and sow productivity (Webb, 1989).

The high proportion of feed costs to total costs of pig production emphasizes the importance of efficient lean meat production. By using a ratio of feed intake over gain, a single trait for efficiency is provided. However, Gunsett (1987) suggested that the heritability of feed to gain ratio may not accurately predict genetic change in feed efficiency. It has been shown that selection for the ratio causes the selection pressure placed on the components to be a function of the selection intensity. As the selection intensity increases, direct selection on the ratio causes the selection to be based primarily on the component in the numerator. Alternative definitions of feed efficiency using a linear index have been suggested as selection criteria for feed efficiency (Gunsett, 1984; Lin, 1980). A genetic analysis of average daily gain, feed intake and feed conversion ratio will therefore be a first step in defining the selection criteria for an efficient lean meat growth.

Predicted feed intake takes requirements for maintenance, growth rate on test and leanness into account and residual feed intake is defined as the difference between predicted and observed feed intake (Foster et al., 1983). Responses to divergent selection on residual feed intake have been demonstrated in hens (Kettle and Kolstad, 1991). In contrast, Cameron and Curran (1994b) concluded that in order to achieve genetic improvement in feed conversion ratio,

residual feed intake is expected to be less effective than selection on feed conversion ratio. Additionally, Kennedy et al. (1993) analysed statistical and genetical properties of residual feed efficiency and concluded that residual feed intake provides no additional genetic information to its component traits that are already used in breeding programs. This trait will therefore not be further considered in this work.

Traditionally, selection has been placed on lean meat content which is associated with reduced meat quality (Kempster et al., 1986) and to a lesser extent eating quality (Wood et al., 1986). Therefore, with increasing leanness, meat quality decreases and it is necessary to include meat quality traits in breeding decisions to guarantee no further deterioration in meat quality. To improve meat quality, objective measurements are required and measurements mostly used are pH recorded shortly after slaughter and ultimate pH as well as colour of the meat and drip loss percentage. In addition, favourable genetic correlations between intramuscular fat content and eating quality traits indicate the possible merit of including intramuscular fat content in selection decisions to improve pork eating quality. (Cameron, 1990b; Lo et al., 1992).

In the following sections, an overview is given of genetic parameters for production, carcass and meat quality traits as well as reproductive traits of the sow. In this context, only traits have been reviewed that are also included in this project and a summary of average literature values of heritabilities and genetic correlations for these traits is presented in the last part of this chapter.

2.2.2 Growth rate and feed efficiency traits

Traditionally, pigs have been selected on phenotypic performance whereas today's breeding programs use BLUP technology in many cases. This technology requires accurate knowledge of genetic parameters for all traits incorporated in the breeding objective and selection index. Over the years many studies have presented genetic parameters for performance traits. A summary of genetic parameters for performance traits and backfat measurements was given by Stewart and Schinkel (1990) incorporating 175 references from Northern America and Europe. This chapter includes therefore only recent estimates of genetic parameters obtained after 1990.

Heritabilities for average daily gain measured on farm (ADGF) averaged 0.23 with a range of 0.06 to 0.31 (Table 2-3). Studies analysing average daily gain measured in test stations (ADGT) show an average heritability of 0.34, with estimates ranging from 0.14 to 0.52. These

estimates are consistent with the average heritability estimate for average daily gain of 0.30 presented by Stewart and Schinkel (1990). However, comparing heritabilities for average daily gain obtained from field data and test station data indicates slightly higher heritabilities for this characteristic measured in test stations. A reduced heritability could be caused by an increased environmental variation which cannot totally be explained by the model used for analysis. An important source of variation for on-farm test results are herd effects. Merks (1989) showed that 10 to 26% of the variance across regions in performance and carcass traits is due to herd differences. Another source of variation for field data originates from different field inspectors. This effect accounted for one to five percent of the total variation for performance and carcass traits (Merks, 1989).

Additionally, field data and test station data often differ in housing conditions. Group housing dominates for on-farm performance recording whereas single penned housing is commonly found in test stations. With more computerized feed intake measurements being used in test stations, group housing has increased allowing analysis of the effect of housing systems on genetic parameters (van Oijen and Merks, 1995; von Felde et al., 1995). Changing the housing system from single housing to group housing led to a decrease in heritability for average daily gain in Dutch Landrace (0.23 vs. 0.09) whereas heritability estimates were increased for Dutch Yorkshire from 0.15 to 0.17 for the dam line and from 0.21 to 0.27 for the sire line (van Oijen and Merks, 1995). In contrast, no changes in heritabilities for average daily gain were found by von Felde et al. (1995) for different housing systems. Change of housing systems was totally confounded with different testing periods in both studies and other factors such as different selection strategies or different types of animals that were sent to the test station over different testing periods could have influenced these results.

Growth performance is influenced by the environment that is common to litter mates, which includes environmental effects from the mother and the pen they share. Its magnitude is shown in the second row in Table 2-3 for each study which included this environmental effect (c^2). For average daily gain measured on farm (ADGF) the mean of c^2 is 0.26, which is higher than the direct genetic effect. In contrast, the magnitude of this effect is lower for average daily gain measured in test stations (ADGT) ($c^2 = 0.15$). Average daily gain on-farm often represents life time average daily gain and includes the preweaning growth period. This period is more strongly influenced by the maternal ability of the sow, thus leading to a stronger effect of the litter on growth performance.

Table 2-3 Literature estimates of heritabilities and litter effects (on the second line) for performance traits

Reference	N	Breed	ADGF	ADGT	FDINT	FCR	LEANG
Johansson et al. (1987a)	8234	LR					0.43
Johansson et al. (1987a)	448	LW					0.46
Cameron (1990)	160	pooled		0.50			0.52
Cameron (1990)	160	pooled		0.44			
Kaplon et al. (1991)	114347	LW	0.27 0.09				
van Steenberg et al. (1990)	2792	pooled		0.30	0.24	0.31	
Keele et al. (1991)	2077	pooled		0.16 0.19			
Cardellino and Siewerdt (1992)	3208	LR	0.25				
Cardellino and Siewerdt (1992)	2437	LW	0.06				
Hovenier et al. (1992)	1113	pooled		0.29			
Hofer et al. (1992)	3 x 10702	Y	0.16 0.42				
Hofer et al. (1992)	3 x 10599	LR	0.20 0.49				
Klassen (1992)	12111	LR	0.31				
Klassen (1992)	12390	LW	0.28				
Lo et al. (1992)	5649	pooled		0.36			
Ducos et al. (1993)	3671	LW		0.30 0.14		0.22 0.09	
Ducos et al. (1993)	3039	LW		0.52 0.14			
Ducos et al. (1993)	3630	LR		0.34 0.14		0.25 0.12	
Ducos et al. (1993)	2695	LR		0.46 0.16			
Mrode & Kennedy (1993)	7562	pooled		0.43	0.45	0.28	0.39
Cameron & Curran (1994b)	2642	LR		0.14	0.19	0.15	
Cameron & Curran (1994b)	3537	LW		0.37	0.29	0.19	
de Vries et al. (1994a)	10454	Y	0.19 0.23				
de Vries et al. (1994a)	13672	LW	0.21 0.17				
de Vries et al. (1994a)	13265	LR	0.24 0.17				
de Vries et al. (1994b)	3279	Y	0.31		0.40		
Roehe et al. (1994)	1212	PIC		0.35	0.26	0.21	
Stern et al. (1994)	2885	Y	0.31				0.39
Stern et al. (1994)	2885	Y	0.35				0.35
Hofer and Schwörer (1995)	4656	LW		0.32 0.15	0.47 0.14	0.46 0.21	
Knapp et al. (1995)	1865	LW		0.27		0.28	
Knapp et al. (1995)	3370	LR		0.21		0.21	
Knapp et al. (1995)	3927	P		0.28		0.23	
weighted ¹ mean of h ²			0.23	0.35	0.36	0.26	0.41
weighted ¹ mean of c ²			0.26	0.15		0.14	

Breeds: LW : Large White, LR: Landrace; Y: Yorkshire, P: Pietrain, PIC: Pig Improvement Company line,

¹ according to N

Heritability estimates for feed intake (FDINT) and feed conversion ratio (FCR) average 0.36 and 0.26, respectively (Table 2-3). Although these values are slightly different than the average heritability estimates for feed intake and for feed efficiency presented by Stewart and Schinkel (1990) (0.24 and 0.30, respectively) the number of studies considered in Table 2-3 is not sufficient to manifest a significant shift in heritabilities for these traits.

Roehe et al. (1994) estimated genetic parameters for daily feed intake over fortnightly intervals for a test period from 100 to 170 days. The first week showed a reduced heritability of 0.13 for feed intake which then increased to 0.39 and 0.45 in the third and fifth week. After this testing period heritabilities dropped to 0.30 and 0.18 for the seventh and ninth week. Roehe et al. (1994) suggested that the lower heritabilities, as well as negative genetic correlations between daily feed intake and average daily gain for the first and third week, are due to bias from numerous unaccountable influences of adaptation of animals to the new feeding device. Heritabilities for feed conversion ratio for the different weeks were higher than the overall estimate for the whole test period ranging from 0.31 in the third week to 0.50 in the fifth week.

A summary of genetic and phenotypic correlations between performance traits recently presented in the literature is given in Table 2-4. Information about genetic correlations between average daily gain measured on-farm (ADGF) with growth rate recorded in a test station (ADGT) is limited. Results from a Dutch study (Merks and van Oijen, 1994) showed genetic correlations ranging between 0.96 and 0.70. These correlations are higher than the estimates presented by Merks (1989) who found a range of 0.3 to 0.6 for genetic correlations between growth rate measured on-farm and average daily gain over a test period. Changes in the environment of the test station which include the introduction of group housing instead of single housing and the switch to ad libitum feeding in contrast to restricted feeding are responsible for the improvement of these genetic correlations (Merks and van Oijen, 1994).

Genetic correlations between average daily gain (ADGT) and feed intake (FDINT) range from 0.37 to 0.80 which is lower than the average given by Stewart and Schinkel (1990) of 0.87 for ad libitum feeding. In the case of restricted feeding, Stewart and Schinkel (1990) presented an average genetic correlation between growth rate and feed intake of 0.57. Phenotypic correlations follow the same pattern with values ranging between 0.41 and 0.78. These are in agreement with the average given by Stewart and Schinkel of 0.75 for ad libitum feeding and 0.40 in the situation of restricted feeding. A high growth rate is therefore accompanied by a high feed intake.

Table 2-4 Literature estimates of genetic (**above diagonal**) and phenotypic correlations (below diagonal) for performance traits

	N	Breed	ADGF	ADGT	FDINT	FCR	LEANG
ADGF							
Merks and van Oijen (1994)		LR		0.96			
Merks and van Oijen (1994)		Y-dam		0.96			
Merks and van Oijen (1994)		Y-sire		0.70			
ADGT							
Lundeheim et al. (1980)	11292	pooled					0.85¹
Johansson et al. (1987a)	8234	LR					0.82¹
Johansson et al. (1987a)	4448	Y					0.80¹
van Steenbergen et al. (1990)	2792	pooled			0.57	-0.58	
Ducos et al. (1993)	3671	LW				-0.46	
						-0.76	
Ducos et al. (1993)	3630	LR				-0.76	
						-0.76	
Mrode & Kennedy (1993)	7562	pooled			0.80	-0.28	0.96
de Vries et al. (1994b)	4055	Y			0.75		
Cameron & Curran (1994b)	2642	LR			0.37	-0.66	
Cameron & Curran (1994b)	3537	LW			0.64	-0.44	
Roehe et al. (1994)	1212	PIC			0.63		
Stern et al. (1994)		Y					0.96
Stern et al. (1994)		Y					0.96
Hofer and Schwörer (1995)	4656	LW			0.76	-0.15	
FDINT							
Lundeheim et al. (1980)	11292	pooled					0.16¹
van Steenbergen et al. (1990)	2792	pooled		0.62		0.33	
Mrode & Kennedy (1993)	7562	pooled		0.74			
Cameron & Curran (1994b)	2642	LR		0.41		0.42	
Cameron & Curran (1994b)	3537	LW		0.76		0.38	
de Vries et al. (1994b)	4055	Y	0.73				
Hofer and Schwörer (1995)	4656	LW		0.78		0.52	
FCR							
Sönnichsen and Kalm (1984b)	4636	pooled		-0.52			
Johansson et al. (1987a)	8234	LR					-0.87¹
Johansson et al. (1987a)	4448	Y					-0.87¹
van Steenbergen et al. (1990)	2792	pooled		-0.47	0.39		
Mrode & Kennedy (1993)	7562	pooled		-0.36			
Cameron & Curran (1994b)	2642	LR		-0.52	0.55		
Cameron & Curran (1994b)	3537	LW		-0.52	0.14		
Hofer and Schwörer (1995)	4656	LW		-0.36	0.25		
LEANG							
Lundeheim et al. (1980)	11292	pooled		0.64	0.22		
Johansson et al. (1987a)	8234	LR		0.96		-0.83	
Johansson et al. (1987a)	4448	Y		0.96		-0.81	
Mrode and Kennedy (1993)	7562	pooled		0.96			

for abbreviations see Table 2-3.; ¹ restricted feeding

In this context, the relationship between growth rate and feed efficiency is important. Genetic and phenotypic correlations between growth rate and feed efficiency range from -0.15 to -0.76 and from -0.36 to -0.52, respectively. The average estimates given by Stewart and Schinkel (1990) fall in this range with estimates of -0.70 for the genetic correlation and -0.52 for the phenotypic correlation. This relationship is favourable, showing that pigs with high growth rate are also more efficient.

Higher feed intake (FDINT) is associated with an increased food conversion ratio (FCR) as genetic and phenotypic correlations show, ranging from 0.33 to 0.52 and 0.14 to 0.55, respectively. Stewart and Schinkel (1990) presented an average estimate for genetic correlations of 0.20 and for phenotypic correlations of 0.22. Although this relationship might become unfavourable, in the situation when a reduced feed intake limits further improvement in lean growth rate (Webb, 1989), its magnitude is still lower than the favourable relationship between average daily gain and feed conversion ratio (Table 2-4). The genetic correlation between these two traits is in the range of -0.15 to -0.76 which is in agreement with the average genetic correlation of -0.70 presented by Stewart and Schinkel (1990). Feed efficiency is defined as the ratio of food consumed to live weight gain and is therefore dependent on these two characteristics. In summary, although faster growing pigs eat more, a proportionally larger amount of food eaten is used for growth rather than maintenance requirements.

To improve lean tissue growth rate, Fowler et al. (1976) proposed a biological approach defining lean tissue growth rate (LEANG) as a selection criterion. Genetic parameters found in the literature for this trait are limited. Mrode and Kennedy (1993) estimated a heritability of 0.39 which is slightly lower than heritabilities presented by Johansson et al. (1987a) (0.43 for Landrace and 0.46 for Yorkshire). Genetic and phenotypic correlations with average daily gain are high, with values ranging from 0.80 to 0.96 (Johansson et al., 1987a; Mrode and Kennedy, 1993).

Variation in genetic parameters due to feeding regime is well established in pigs (Wyllie et al., 1979). Comparing heritability estimates for performance traits under ad libitum and under restricted feeding regimes, estimates were found to be lower in the situation of ad libitum feeding (McPhee et al., 1988; Cameron et al., 1988). Despite the higher genetic variation found in the situation of ad libitum feeding, residual variances were also increased substantially leading to lower heritabilities for average daily gain and feed conversion ratio (Cameron et al., 1988). These experiments were conducted in single pen housing systems and Cameron (1990b) suggested that heritabilities for average daily gain are lower in a restricted feeding situation with group penning, as competition between pen mates would increase non-additive variance

components. Genetic correlations between average daily gain and feed efficiency were found to be stronger under restricted feeding than under ad libitum feeding (Cameron et al., 1988; Johansson et al., 1987a). However, no sire by feeding regime interaction was detected in Large White pigs for average daily gain or feed conversion ratio (Cameron et al., 1988).

2.2.3 Carcase traits

Besides increasing growth rate, genetic improvement of pigs has also been focusing on improving leanness in pigs and good genetic response due to selection has been achieved. Stewart and Schinkel (1990) reported an average heritability for backfat of 0.41 and for lean meat percentage of 0.48 in their review. The summary of heritabilities presented in Table 2-5 includes therefore only studies after 1990 and studies analysing additional carcase traits such as loin area, ham weight or weight of primary cuts.

Generally, backfat (BF) is highly heritable, with an average heritability for this trait of 0.43 across studies (Table 2-5). Additionally, estimates of litter effect (c^2) are also very consistent between presented studies with an average of 0.10. Merks and van Oijen (1994) found genetic parameters for backfat recorded in different testing environments. Heritability estimates were higher in the field testing program than in the central station test. Generally, genetic correlations between the two environments were high (0.87 to 0.97) which was slightly higher than the genetic correlation obtained by Merks (1989) for the same breeds, thus showing good agreement between backfat measured on-farm and in test stations. In addition, housing system has a minor effect on genetic parameters for backfat. This was shown by von Felde et al. (1995) who found a genetic correlation of 0.79 for backfat measured in single penned housing and group housing.

Although backfat is mostly recorded, lean meat percentage (LEAN) is regarded as the more precise evaluation of the carcase value (Ferguson, 1995). Lean meat percentage is either derived by dissection (Hovenier et al., 1992) or through prediction equations including live weight, loin muscle area, average backfat thickness and carcase length (Lundeheim et al., 1980). Another prediction equation is based on percentages of ham, loin, backfat, leaf fat, belly and shoulder (Ducos et al., 1993). Although lean meat percentage was derived in different manners, estimates of heritabilities are consistently high with values ranging from 0.41 to 0.93. In addition, further carcase traits such as loin area and ham weight or primary cuts have high heritabilities with an average of 0.51 for loin area and a range of heritabilities of 0.36 to 0.60 for ham weight and primary cuts (Table 2-5).

Table 2-5 Literature estimates of heritabilities and litter effects (in c^2 column) for carcass traits

Reference	N	Breed	BF	BF c^2	Loin area	LEAN	HAM	HAM c^2
Lundeheim et al. (1980)	11292	pooled			0.49	0.68		
Just et al. (1983)			0.41		0.44	0.41		
Ollivier (1983)	2736	pooled					0.41	
Sönnichsen and Kalm (1984a)	4636	pooled					0.36	
Johansson et al. (1987a,b)	8234	LR				0.78	0.43	
Johansson et al. (1987a,b)	4448	Y				0.93	0.43	
Cameron (1990a)	320	pool	0.52			0.63		
Kaplon et al. (1990)	114347	LW	0.29	0.10				
van Steenberg et al. (1990)	2792	pooled	0.37					
Keele et al. (1991)	1953	pooled	0.56	0.09				
Cardellino and Siewerdt (1992)	3208	LR	0.15					
Cardellino and Siewerdt (1992)	2437	LW	0.13					
Hovenier et al. (1992)	1113	pooled	0.51			0.63		
Lo et al. (1992)	4647	pooled	0.54 ²		0.46 ²			
			0.56		0.80			
Hofer et al. (1992)	3 x 10702	Y					0.44 ¹	0.16
Hofer et al. (1992)	3 x 10599	LR					0.42 ¹	0.16
Klassen (1992)	12111	LR	0.56					
Klassen (1992)	12390	LW	0.48					
Scholz and Triebler (1992)	5450	LEIC.	0.40		0.48		0.55 ¹	
Scholz and Triebler (1992)	10102	SCHW.	0.34		0.46		0.41 ¹	
Ducos et al. (1993)	3671	LW	0.64	0.05				
Ducos et al. (1993)	3039	LW				0.60		
						0.13 ³		
Ducos et al. (1993)	3630	LR	0.56	0.12				
Ducos et al. (1993)	2695	LR				0.68		
						0.09 ³		
Bidanel et al. (1994a)	1276	P	0.45	0.09				
de Vries et al. (1994a)	10454	Y	0.43	0.16				
de Vries et al. (1994a)	3672	LW	0.45	0.07				
de Vries et al. (1994a)	3265	LR	0.53	0.06				
de Vries et al. (1994b)	4055	Y				0.52		
Li and Kennedy (1994)	47360	Y	0.51	0.11				
Li and Kennedy (1994)	28762	LR	0.53	0.10				
Li and Kennedy (1994)	14020	Duroc	0.55	0.10				
Li and Kennedy (1994)	9983	Ha	0.50	0.11				
Roehe et al. (1994)	1212	PIC	0.58					
Cameron and Curran (1994b)	2642	LR	0.25					
Cameron and Curran (1994b)	3537	LW	0.46					
Hofer and Schwörer (1995)	4656	LW					0.60 ¹	0.06
weighted mean (according to N)			0.43	0.10	0.51	0.70		0.44

second row is c^2 effect; ¹ primary cuts, ² first row ultrasound measurement, second row carcass measurement; ³ litter effects; Breed abbreviations: see Table 2-3, Ha: Hampshire, SCHW.: Schwerfurter, LEIC. Leicoma, (the last two breeds are synthetic lines developed in the former German Democratic Republic)

Cameron et al. (1988) and Cameron (1990a) estimated heritabilities for backfat under restricted and ad libitum feeding regimes. Heritability estimates for ultrasonic backfat depth

dropped from 0.72 under an ad libitum feeding regime to 0.19 under a restricted feeding regime (Cameron et al., 1988). In a designed experiment with 40 litters Cameron (1990a) estimated heritabilities for backfat of 0.40 for ad libitum feeding and 0.32 for restricted feeding regime. Cameron et al. (1988) suggested that this change of estimates might be due to the reduction in the ability of pigs to express their genetic potential for subcutaneous fat under restricted feeding.

Table 2-6 Literature estimates of genetic (*above diagonal*) and phenotypic correlations between carcass traits

	N	Breed	BF	Loin area	LEAN	HAM
Backfat (BF)						
Lundeheim et al. (1980)	11292	pooled		-0.26	-0.86	
Schwörer et al. (1980)	2630	LW				-0.93 ¹
Schwörer et al. (1980)	1567	LR				-0.95 ¹
Ollivier (1983)	2736	pooled				-0.23
Sönnichsen and Kalm. (1984b)	4636	pooled				-0.46
Cameron et al. (1990)	320	pooled			-0.94	
Hovenier et al. (1992)	1113	pooled			-0.71	
Lo et al. (1992)	4647	pooled		-0.56 ²		
Lo et al. (1992)	4647	pooled		-0.81 ³		
Lo et al. (1992)	4647	pooled		-0.72 ⁴		
Loin area						
Lundeheim et al. (1980)	11292	pooled	-0.20		0.66	
Lo et al. (1992)	4647	pooled	-0.45 ²			
Lo et al. (1992)	4647	pooled	-0.82 ³			
Lo et al. (1992)	4647	pooled	-0.31 ⁴			
Lean meat percentage (LEAN)						
Lundeheim et al. (1980)	11292	pooled	-0.82	0.66		
Johansson et al. (1987b)	8234	LR				0.46
Johansson et al. (1987b)	4448	Y				0.45
Cameron (1990)	320	pooled	-0.20			
Hovenier et al. (1992)	1113	pooled	-0.75			
Ham (HAM)						
Ollivier (1983)	2736	pooled	-0.13			
Sönnichsen and Kalm (1984b)	4636	pooled	-0.30			
Johansson et al. (1987b)	8234	LR			0.48	
Johansson et al. (1987b)	4448	Y			0.61	

¹ premium cuts;

² Ultrasound BF- Ultrasound Muscle depth (MD);³Carcass BF - Ultrasound MD; ⁴Ultrasound BF - Carcass MD

Lo et al. (1992) included real time ultrasound and carcass measurements in their analyses. Although estimates for real time ultrasound measurements were slightly lower, especially for loin muscle area, their magnitude was still high, indicating the close relationship between

measurement on the live animal and carcass characteristics. This finding is strengthened by high genetic and phenotypic correlations between ultrasound measurement and carcass measurements of 0.85 and 0.71 for backfat, and 0.87 and 0.75 for loin area.

Carcass backfat is used as an indicator of carcass leanness because it is easy to measure. Its close relationship to carcass leanness was demonstrated by Stewart and Schinkel (1990) who reported genetic and phenotypic correlations of -0.85 and -0.71 between backfat and lean meat content in their review. Correlations between backfat and lean meat percentage presented in Table 2-6 are of the same magnitude. Additionally, backfat is highly related to loin area and primary cuts as shown by Schwörer et al. (1980) and Lo et al. (1992). The lower association between fat depth and loin area found by Lundeheim et al. (1980) might be due to different measurement techniques. However, the relationship between muscle depth and lean meat percentage presented by Lundeheim et al. (1980) was moderate. Weight of the ham (HAM) is a further valuable part of the carcass and estimates of genetic correlations with backfat and lean meat percentage are presented in Table 2-6. Although only a few studies are available, results across studies are consistent with the absolute magnitude of genetic correlations ranging from 0.23 to 0.46 and the absolute value of phenotypic correlations being in the range from 0.13 to 0.61.

2.2.4 Meat quality traits

Over the last few years there has been much discussion on how to incorporate meat quality into breeding programs. Incorporation of meat quality traits into breeding programs requires knowledge of genetic parameters which were reviewed for meat quality characteristics by Sellier (1988), Schwörer et al. (1990) and Hovenier et al. (1993). Average heritability estimates from these studies and heritabilities obtained after 1990 are presented in Table 2-7 for meat quality traits.

Heritability estimates reviewed by Sellier (1988) and Hovenier et al. (1993) for pH measurements taken 45 minutes after slaughter (pH45) and 24 hours post mortem (pH24) averaged 0.18 and 0.30, and 0.22 and 0.20, respectively. Estimates obtained in recent studies are slightly lower with an overall average of 0.20 (pH45) and 0.17 (pH24).

Low estimates of heritabilities were found by Bidanel et al. (1994a) in Pietrain pigs for both pH measurements as well as drip loss percentage (DLP) in contrast to an estimate of 0.20 which was presented by de Vries et al. (1994b) for Dutch Yorkshire. The later estimate is in

agreement with the average value given by Hovenier et al. (1993) and slightly higher than the average value presented by Sellier (1988) of 0.12. Hovenier et al. (1993) reported a range of 0.00 to 0.63 for heritability estimates for drip loss percentage. This large range might have been due to different measurement techniques. Different measurement techniques could also explain different heritabilities for cooking loss varying from 0.06 to 0.24 (Table 2-7).

Colour has a mean heritability of 0.24 based on recent studies presented in Table 2-7 which is slightly lower than average values given by Sellier (1988) and Hovenier et al. (1993). Although Hovenier et al. (1993) reported no influence of measurement technique on heritability estimates for colour, the lower heritability of 0.11 presented by Lo et al. (1992) might have been caused by the measurement system consisting of a scoring system ranging from 1 to 3. In the review by Hovenier et al. (1993) mean estimates of heritabilities for meat colour were 0.35 for Landrace and 0.30 for Large White.

Table 2-7 Literature estimates of heritabilities for meat quality traits

			pH45	pH24	Colour	DLP	Cook. Loss.	IMF
Review by:			average literature values					
Sellier (1988)			0.18	0.22	0.27	0.12		0.51
Schwörer et al. (1990)								0.49
Hovenier et al. (1993)			0.30	0.20	0.30	0.20		0.50
Recent studies	N	breed¹	pH45	pH24	Colour	DLP	Cook Loss	IMF
Cameron (1990b)	320	pooled		0.20	0.20			0.53
Hovenier et al. (1992)	1113	pooled						
Lo et al. (1992)	792	pooled		0.14	0.11		0.06	0.52
de Vries et al. (1994b)	4055	Y	0.15	0.15	0.21	0.20	0.11	0.41
Bidanel et al. (1994a)	1276	P	0.04	0.07		0.07	0.24	
Bidanel et al. (1994b)	6358	LW		0.17				
Bidanel et al. (1994b)	3538	LR		0.14				
Goodwin (1994)	2111	pooled		0.35	0.37		0.22	0.61
Hofer and Schwörer (1995)	4656	LW	0.29	0.16	0.22			0.51
Knapp et al. (1995)	1865	LW						0.39
Knapp et al. (1995)	3370	LR						0.36
Knapp et al. (1995)	3927	P						0.45
weighted mean (according to N)			0.20	0.17	0.24	0.17	0.15	0.45

¹ For breed abbreviations see Table 2-3,

Estimates of heritabilities for intramuscular fat content (IMF) from recent studies averaged 0.45 which is in good agreement with mean heritability estimates presented by Sellier (1988), Schwörer et al. (1990) and Hovenier et al., (1993). Estimates vary from 0.36 to 0.61 between

studies presented in Table 2-7 while Schwörer et al. (1990) found a larger variation between studies ranging from 0.26 to 0.83.

Ducos et al. (1993) estimated heritabilities for a meat quality index including ultimate pH, water holding capacity and reflectance value. Estimates were 0.33 for Large White and 0.23 for French Landrace. Knapp et al. (1995) obtained heritabilities of 0.16 for Large White, 0.15 for Landrace and 0.12 for Pietrain pigs for a meat quality index including colour, pH recorded at 45 minutes after slaughter and drip loss percentage.

Bidanel et al. (1994b) estimated heritabilities for ultimate pH in various muscles. Heritabilities were slightly higher for *m. semispinalis* (0.22 for Large White and 0.18 for French Landrace), a red muscle with a high oxidative activity and a high ultimate pH, than for the *m. adductor femoris* and *m. semimembranosus*, which are both white muscles with a low oxidative activity and a low ultimate pH. Common environmental effects had low estimates of 0.02 for Large White and 0.06 for French Landrace. Genetic correlations between the two white muscles were 0.99 for Large White and for French Landrace. In contrast genetic associations between *m. semispinalis* and the two white muscles were lower with genetic correlations varying from 0.73 to 0.82 for the two breeds.

Measuring pH at 45 minutes after slaughter (pH45) and ultimate pH (pH24) gives information about PSE and DFD status of meat. Although these two deficiencies have different causes the two pH measurements are positively correlated (Table 2-8). A high pH45 and therefore a low incidence of PSE is associated with a high pH24 which is an indication for DFD meat.

The optimum for these traits is a medium range to prevent PSE and DFD. Characteristics of PSE meat are a pale colour and a high drip loss. These associations are reflected in genetic correlations between pH45 and colour and drip loss percentage. Colour is expressed as a reflectance value and high measurements represent a light colour of the meat and genetic correlations between -0.38 and -0.70 show that pH45 is associated with a pale colour. In connection with a low pH45 only de Vries et al. (1994b) estimated a moderate correlation for increased drip loss (-0.55) and enlarged cooking loss (-0.23). In contrast, Bidanel et al. (1994a) found no relationship between pH45 and drip loss percentage and cooking loss for Pietrain pigs.

Table 2-8 Literature estimates of genetic (*above diagonal*) and phenotypic correlations between meat quality

References	N	breed ¹	pH45	pH24	Colour	DLP	Cook Loss	IMF
pH45								
Bidanel et al. (1994a)	1276	P		0.49		0.01	0.04	
de Vries et al. (1994b)	4055	Y		0.10	-0.55			
de Vries et al. (1994b)	1807	Y		0.15	-0.38	-0.55	-0.23	-0.04
Hofer and Schwörer (1995)	4656	LW		0.43	-0.70			0.36
pH24								
Johansson et al. (1987b)	8234	LR			-0.41			
Johansson et al. (1987b)	4448	Y			-0.21			
Cole et al. (1988)	8867	LW			-0.08	0.47²		
Cole et al. (1988)	4098	LR			-0.71	0.54²		
Cole et al. (1988)	2840	B-LR				0.30²		
Cameron (1990b)	320	pooled			-0.38			0.39
Hovenier et al. (1992)	1113	pooled			0.73³	-0.80		-0.18
Bidanel et al. (1994a)	1276	P	0.01			-0.99	-0.72	
de Vries et al. (1994b)	4055	Y	0.20		-0.65			
de Vries et al. (1994b)	1087	Y	0.15		-0.60	-0.54	-0.82	-0.05
Goodwin (1995)	2111	pooled			-0.30			0.04
Hofer and Schwörer (1995)	4656	LW	0.18		-0.36			0.24
Colour								
Malmfors and Nilsson (1979)	978	Y				-0.06	0.32	
Johansson et al. (1987b)	8234	LR		-0.12				
Johansson et al. (1987b)	4448	Y		0.06				
Cole et al. (1988)	8867	LW		-0.29		-0.71²		
Cole et al. (1988)	4098	LR		-0.30		-0.81²		
Cole et al. (1988)	2840	B-LR		-0.43				
Cameron (1990b)	320	pooled		-0.29				-0.12
Hovenier et al. (1992)	1113	pooled		0.43		-0.73³		-0.33
de Vries et al. (1994b)	4055	Y	-0.31	-0.32				
de Vries et al. (1994b)	1087	Y	-0.23	-0.44		0.49	0.47	-0.10
Goodwin (1995)	2111	pooled						0.07
Hofer and Schwörer (1995)	4656	LW	-0.49	-0.30				-0.08
Drip loss percentage (DLP)								
Malmfors and Nilsson (1979)	978	Y			0.15		0.66	
Cole et al. (1988)	8867	LW			-0.37			
Cole et al. (1988)	4098	LR			-0.50			
Cole et al. (1988)	2840	B-LR			-0.52			
Hovenier et al. (1992)	1113	pooled		-0.46	-0.36			-0.07
Bidanel et al. (1994a)	1276	P	-0.10	0.00			0.75	
de Vries et al. (1994b)	1087	Y	-0.45	-0.47	0.52		0.45	-0.23
Cooking loss (Cook. Loss)								
Malmfors and Nilsson (1979)	978	Y				0.19		
Bidanel et al. (1994a)	1276	P	-0.10	-0.20		0.34		
de Vries et al. (1994b)	1087	Y	-0.10	-0.56	0.32	0.39		-0.03
Intramuscular fat content (IMF)								
Cameron (1990b)	320	pooled		0.11	-0.06			
Hovenier et al. (1992)	1113	pooled		-0.09	-0.11 ³	-0.03		
de Vries et al. (1994b)	1087	Y	-0.03	0.04	0.08	-0.03	-0.09	
Hofer and Schwörer (1995)	4656	LW	0.13	0.07	0.01			

¹ for breed abbreviations see Table 2-1 ² water holding capacity; ³ colour scoring is of opposite sign

Ultimate pH (pH₂₄) gives information about the incidence of DFD meat and a higher pH₂₄ is associated with a darker colour of the meat and a reduced drip loss. These relationships are well reflected in genetic correlations between these traits, although the signs of correlations differ due to different measurement techniques. Hovenier et al. (1992) used a scoring system to describe colour with lower values representing lighter colour, in contrast to reflectance measurements where higher values reflect paler meat. Although of different signs, genetic correlations between ultimate pH and colour measurements reflect therefore the same relationship, with higher pH values being related to a darker colour. Absolute values of genetic correlations vary from 0.08 to 0.73. Genetic and phenotypic correlations between pH₂₄ and drip loss percentage also have to be looked at in absolute terms, as Cole et al. (1988) recorded water holding capacity in contrast to drip loss percentage. A high ultimate pH is therefore strongly related to low drip loss percentage, which is equivalent to a high water holding capacity and a reduced cooking loss. The range of genetic correlation between ultimate pH and drip loss percentage is 0.47 to 0.99 in absolute terms, and -0.72 and -0.82 between ultimate pH and cooking loss.

Genetic and phenotypic correlations between intramuscular fat content and pH measurements are inconsistent between studies. The two Dutch studies (Hovenier et al., 1992; de Vries et al., 1994b) found slightly negative genetic correlations between fat content and pH measurements. In contrast, intramuscular fat content is associated with a higher pH in other studies (Cameron, 1990b; Goodwin, 1995; Hofer and Schwörer, 1995) with a range of 0.04 to 0.39. With the exception of Goodwin (1995), who found a slightly positive genetic correlation between colour and intramuscular fat content, genetic relationships between intramuscular fat content and the other meat quality traits; colour, drip loss and cooking loss are in agreement between studies. A reduced intramuscular fat content is associated with a lighter colour, a higher drip loss and increased cooking loss. The range of estimated genetic correlations is -0.03 to -0.33 for these trait combinations.

Drip loss percentage and cooking loss exhibit similar associations to other meat quality characteristics and their close relationship is demonstrated through genetic correlations ranging from 0.45 to 0.75 between studies.

2.2.5 Growth, carcass and meat quality traits

Genetic evaluation of farm animals is based on multitrait BLUP procedures incorporating information from different traits including growth performance, carcass traits and meat quality

characteristics. Knowledge about genetic associations between all traits included in the multitrait evaluation is required. Average daily gain and backfat are the two traits most commonly incorporated in selection decisions and their genetic relationship has been analysed frequently (Table 2-9.). High average daily gain (ADG) is associated with an increased backfat on ad libitum feeding. Genetic and phenotypic relationships between average daily gain and backfat vary between 0.19 and 0.83, and 0.03 to 0.28. The only significant negative genetic correlation between these two traits was found by Cameron and Curran (1994b) for Landrace pigs, but no explanation was given for this discrepancy. In their review, Stewart and Schinkel (1990) found an average genetic correlation between growth performance and backfat of 0.22 and a slightly lower phenotypic correlation of 0.20.

Due to the close relationship between backfat and lean meat percentage and growth rate, the mean genetic and phenotypic correlation of -0.15 and -0.11 between growth rate and lean meat content summarized by Stewart and Schinkel (1990) is expected. In more recent studies, Ducos et al. (1993) and de Vries et al. (1994b) found genetic correlations between lean meat percentage and growth rate of -0.06 for French Landrace and -0.34 for Dutch Yorkshire in ad libitum feeding systems. This unfavourable relationship is not present in a restricted feeding regime. In Swedish studies undertaken by Lundeheim et al. (1980) and Johansson et al. (1987b), which were based on restricted feeding regimes, genetic correlations between growth rate and leanness ranged from 0.31 to 0.53. In a selection experiment, Cameron et al. (1994) found slightly negative genetic correlations between average daily gain and backfat of -0.10 and -0.02 for Large White and Landrace, respectively. This confirms results from McPhee et al. (1988) who found a positive genetic correlation (0.35) between average daily gain and backfat on ad libitum feeding and a negative genetic correlation (-0.22) on restricted feeding. These estimates were obtained in single penned housing systems and Cameron (1990a) suggested that genetic correlations between growth rate and backfat depth for pigs fed at a restricted level would be increased by the effect of competition in a group penned situation, as more dominant pigs would be faster growing and fatter due to relatively greater food intakes than their pen mates.

Increased lean meat percentage is associated with a larger loin eye area and larger weights of ham and primary cuts. An influence of feeding regime is not apparent between muscle depth and growth rate. Both studies included in Table 2-9 show negative genetic correlations of -0.16 and -0.18 between these two traits. These estimates were obtained in a restricted feeding regime (Lundeheim et al., 1980) while the study of Lo et al. (1992) was based on an ad libitum feeding system. However, genetic correlations between ham weight and growth rate were influenced by the feeding system. In restricted feeding, Johansson et al. (1987b) obtained a

positive and favourable genetic relationship between ham weight and growth rate (0.16 for Landrace and 0.25 for Yorkshire) in contrast to other studies shown in Table 2-9 which obtained genetic parameters between growth rate and carcass traits on ad libitum feeding. Genetic correlations for these studies (Sönnichsen and Kalm, 1984b; Hofer et al., 1992; Hofer and Schwörer, 1995) are in the range of -0.13 to -0.33.

The importance of considering feed intake (FDINT) in selection programs to avoid further reduction in this characteristic has been shown by Brandt (1987). Genetic correlations between feed intake and carcass characteristics summarized in Table 2-9 show that selection for reduced backfat leads to a reduced feed intake. The magnitude of this relationship varies from 0.24 to 0.51 for genetic correlations and from 0.13 and 0.39 for phenotypic correlations. The genetic correlation between lean meat percentage and feed intake was -0.48 in a Dutch study (de Vries et al., 1994b) and is even stronger (-0.72) between primary cut weights and feed intake (Hofer and Schwörer, 1995).

Genetic correlations between feed conversion ratio (FCR) and carcass characteristics are generally favourable with values varying between 0.18 and 0.36 for backfat, and ranging from -0.30 to -0.55 for lean meat percentage. Reducing feed intake while keeping average daily gain constant is one way of improving feed efficiency. Since genetic correlations between feed intake and carcass characteristics are of higher magnitude than genetic correlations between average daily gain and carcass traits, improvement in feed efficiency with increasing leanness is due to a reduction in feed intake.

Lean growth rate exhibits no significant genetic association with backfat in the study undertaken by Mrode and Kennedy (1993) while genetic correlations between lean growth rate and lean meat percentage range from 0.77 to 0.95 for the three Swedish studies. These traits are very similar and these high genetic correlations are therefore expected. The genetic correlation between muscle area and lean growth rate is moderate (0.47) (Lundeheim et al., 1980).

Table 2-9 Literature estimates of genetic (first row) and phenotypic correlations (second row) between production and carcass traits

	N	Breed ¹	ADG gen.	ADG phen.	FDINT	FCR	LEANG
Backfat							
Cameron (1990a)	160	pooled	0.83	0.14			
Cameron (1990a)	160	pooled	0.64 ³	0.42			
Kaplon et al. (1990)	114347	LW	0.25	0.23			
van Steenberg et al. (1990)	2792	pooled	0.19	0.20	0.39	0.18	
					0.37	0.14	
Cardellino and Siewerdt (1992)	3208	LR	-0.02				
Cardellino and Siewerdt (1992)	2437	LW	0.24				
Lo et al. (1992)	4647	pooled	0.43 ²	0.03			
Lo et al. (1992)	4647	pooled	0.28	0.21			
Ducos et al. (1993)	3671	LW	0.48	0.24			
Ducos et al. (1993)	3630	LR	0.25	0.11			
Mrode & Kennedy (1993)	7562	pooled	0.32	0.28	0.42	0.24	0.02
					0.33	0.09	0.11
Cameron & Curran (1994b)	2642	LR	-0.25	-0.03	0.24	0.36	
					0.13	0.14	
Cameron & Curran (1994b)	3537	LW	0.26	0.25	0.51	0.27	
					0.39	0.15	
Goodwin (1995)	2111	pooled	-0.04				
Lean meat percentage							
Lundeheim et al. (1980)	11292	pooled	0.31 ³	0.18		-0.30	0.77
						-0.26	0.64
Johansson et al. (1987b)	8234	LR	0.31 ³	0.13		-0.44	0.79
						-0.14	0.35
Johansson et al. (1987b)	4448	Y	0.53 ³	-0.50		-0.55	0.95
						0.16	-0.43
Ducos et al. (1993)	3039	LW	-0.09	-0.19		-0.41	
Ducos et al. (1993)	2695	LR	-0.06	-0.02		-0.22	
de Vries et al. (1994b)	4055	Y	-0.34	-0.36	-0.48		
					-0.42		
Loin eye area							
Lundeheim et al. (1980)	11292	pooled	-0.16	0.09		-0.19	0.47
						-0.16	0.40
Lo et al. (1992)	4647	pooled	-0.18	-0.06			
Ham and primary cut weights							
Sönnichsen and Kalm (1984b)	4636	pooled	-0.21	-0.05		-0.38	
						-0.15	
Johansson et al. (1987b)	8234	LR	0.16 ³				
Johansson et al. (1987b)	4448	Y	0.25 ³				
Hofer et al. (1992)	3 x 10702	Y	-0.13	-0.16			
Hofer et al. (1992)	3 x 10599	LR	-0.18	-0.12			
Hofer and Schwörer (1995)	4656	LW	-0.33	-0.22	-0.72	-0.66	
					-0.62	-0.59	

¹ for breed abbreviations see Table 2-3; ² backfat measured with real time ultrasound; ³ restr. feeding regime;

Hovenier et al. (1993) found a wide range of genetic correlations between meat quality traits and other economically important traits which are summarized in Table 2-10. The first indicator for PSE meat, pH45 has low genetic correlations with performance and feed efficiency traits which range from -0.14 for average daily gain (de Vries et al., 1994b) to 0.14 for feed efficiency (Hofer and Schwörer, 1995). The opposite sign of genetic correlations between studies for each trait and the low magnitude of these parameters suggests that pH45 has no significant genetic correlation with growth rate and feed efficiency.

Genetic correlations range from -0.17 to 0.26 for ultimate pH (pH24) and average daily gain (Table 2-10.). Hovenier et al. (1993) reported a range of -0.23 to 0.50 for this trait combination. The negative genetic correlation between these two traits found by Johansson et al. (1987b) could be due to the restricted feeding system, since all other studies summarized in Table 2-10 are based on ad libitum feeding regimes. However, the genetic correlation (-0.08) found by Cole et al. (1988) for Large White cannot be explained this way. Both studies analysing feed intake and pH24 (de Vries et al., 1994b; Hofer and Schwörer, 1995) showed a positive genetic correlation of 0.12 for this trait combination. Feed efficiency is slightly negatively correlated with pH24 (Hofer and Schwörer, 1995).

In contrast to other meat quality traits, genetic correlations between colour and production traits are consistent between studies, ranging from 0.04 to 0.50 for average daily gain, from 0.01 to 0.14 for feed intake, and from -0.09 to -0.13 for feed efficiency. A paler colour of the meat is therefore associated with a higher growth rate, a slightly higher feed intake and an improved feed efficiency. Hovenier et al. (1993) reviewed genetic correlations between colour and average daily gain. Estimates were in the range of -0.50 to 0.12 thus different from these recent studies summarized in Table 2-10 which might be explained by different measurement techniques for colour in recent studies.

Table 2-10 Literature estimates of genetic (first row) and phenotypic correlations (second row) between production and meat quality traits

	N	Breed ¹	ADG gen.	ADG phen.	FDINT	FCR	LEANG
pH45							
de Vries et al. (1994b)	4055	Y	0.14	0.00	0.04		
Hofer and Schwörer (1995)	4656	LW	-0.02	0.03	0.04	-0.08	-0.14
pH24							
Johansson (1987b)	8234	LR	-0.17 ²	0.05 ²			
Johansson (1987b)	4448	Y	-0.14 ²	0.00 ²			
Cole et al. (1988)	8867	LW	-0.08				
Cole et al. (1988)	4098	LR	0.26				
Cole et al. (1988)	2840	B-LR	0.10				
de Vries et al. (1994b)	4055	Y	0.00	0.06	0.12		
Goodwin (1995)	2111	pooled	0.03		0.12		
Hofer and Schwörer (1995)	4656	LW	0.15	-0.04	0.12		-0.04
Colour							
Lundeheim et al. (1980)	11292	pooled	0.11 ²	0.14 ²		-0.13	0.14
Johansson (1987b)	8234	LR	0.40 ²	0.01 ²		-0.11	0.12
Johansson (1987b)	4448	Y	0.50 ²	-0.04 ²			
Cole et al. (1988)	8867	LW	0.35				
Cole et al. (1988)	4098	LR	0.09				
de Vries et al. (1994b)	4055	Y	0.21	0.02	-0.24		
Goodwin (1995)	2111	pooled	0.41		-0.05		
Hofer and Schwörer (1995)	4656	LW	0.04	0.11	-0.02		-0.09
Drip loss percentage							
Cole et al. (1988)	8867	LW	-0.48 ³				
Cole et al. (1988)	4098	LR	-0.28 ³				
Cole et al. (1988)	2840	B-LR	0.55 ³				
de Vries et al. (1994b)	4055	Y	-0.07	-0.03	-0.35		
					-0.11		
Cooking loss							
de Vries et al. (1994b)	4055	Y	-0.05	-0.10	-0.10		
					-0.12		
Intramuscular fat content							
Lo et al. (1992)	960	pooled	0.27	0.06			
de Vries et al. (1994b)	4055	Y	-0.09	0.15	0.22		
Goodwin (1995)	2111	pooled	-0.03		0.21		
Hofer and Schwörer (1995)	4656	LW	0.11	0.07	0.21		0.16
Knapp et al. (1995)	1865	LW	0.36	0.15			0.12
Knapp et al. (1995)	3370	LR	-0.16	0.10			0.02
Knapp et al. (1995)	3927	P	0.28	0.27			0.07
							0.03
							-0.27
							-0.23

¹ for breed abbreviations see Table 2-3. ² restricted feeding; ³ water holding capacity

Genetic correlations showed a wide range for water holding capacity and average daily gain in the review presented by Hovenier et al. (1993) with estimates ranging from -0.70 to 0.55. Therefore the wide range of estimates for this trait combination presented in Table 2-10 agrees with Hovenier et al. (1993). Cole et al. (1988) recorded water holding capacity instead of drip loss percentage and genetic correlations are therefore of opposite sign in comparison to the estimate obtained by de Vries et al. (1994b). Genetic correlations for Large White and Landrace indicate an increased drip loss percentage with improvement of average daily gain with estimates being 0.48 and 0.28 in absolute terms. In contrast, increasing average daily gain in Belgian Landrace (Cole et al., 1988) and Yorkshire (de Vries et al., 1994b) will increase drip loss percentage or reduce water holding capacity. The magnitude of these relationships is 0.55 for Belgian Landrace and 0.07 for Yorkshire in absolute values. De Vries et al. (1994b) also estimated the genetic relationship between drip loss percentage and feed intake. A high feed intake in this study is associated with a reduced drip loss percentage (-0.35). Parameter estimates for cooking loss, as analysed by de Vries et al. (1994b), follows the same patterns as drip loss percentage, although estimates were slightly lower.

Although the range of genetic parameters between intramuscular fat content and average daily gain lies between -0.16 and 0.36, estimates are mostly above zero, indicating that intramuscular fat content is increased with higher average daily gain. Hovenier et al. (1993) found only positive associations between these traits (0.12 to 0.60). In addition, Schwörer et al. (1990) summarized genetic correlations between intramuscular fat content and production and processing traits. Looking at ten studies, Schwörer et al. (1990) found an average genetic correlation of 0.35 between average daily gain and intramuscular fat content with a range of estimates between 0.14 and 0.44.

The relationship between intramuscular fat content and feed intake has not been reviewed, but the two studies included in Table 2-10 are in good agreement, indicating that a high feed intake is associated with a higher intramuscular fat content. The majority of studies found a positive but unfavourable relationship with feed efficiency. Hovenier et al. (1993) mentioned an average of estimates of 0.10 with a range of -0.34 to 0.36 for genetic correlations and a range of -0.14 to -0.15 for phenotypic correlations between intramuscular fat content and feed efficiency. Schwörer et al. (1990) included four studies, which had genetic correlations between these two traits analysed. The range of these estimates was between -0.20 and 0.30 with an average of -0.07, in contrast to the finding of Hovenier et al. (1993).

Phenotypic correlations between meat quality traits and production traits have not been mentioned explicitly since they follow the same patterns as corresponding genetic correlations.

The magnitude of these phenotypic relationships is lower than genetic correlations between traits and in many cases not significantly different from zero.

The detrimental effect of increasing leanness on meat quality characteristics is well known and is also confirmed by results from studies summarized in Table 2-11. Increasing leanness, by decreasing backfat, reduces pH₄₅ and therefore will increase the incidence of PSE (Bidanel et al., 1994a). A reduction in backfat will also decrease ultimate pH for most breeds with genetic correlations ranging between 0.00 and 0.20. In contrast, Cole et al. (1988) found negative genetic correlations between backfat and ultimate pH for French Landrace and Belgian Landrace, indicating that a reduction in backfat can also lead to DFD meat in extreme meaty type pigs. Estimates of genetic correlations between colour and backfat range between -0.10 and 0.05 (Table 2-11). Thus, showing that decreasing backfat will have little effect on colour but will increase drip loss percentage and estimates of genetic correlations range from 0.06 to 0.20 in absolute terms. All studies found a positive but unfavourable relationship between backfat and intramuscular fat content. This is in agreement with the mean genetic correlation of 0.08 summarized by Schwörer et al. (1990).

Hovenier et al. (1993) found considerable variation in genetic correlations between backfat and meat quality traits, but a reduced backfat is generally associated with inferior meat quality. The trait combination which showed the largest variation was drip loss percentage and different measurement techniques might be responsible for this. In addition to backfat, Hovenier et al. (1993) also summarized genetic and phenotypic correlations between lean meat percentage and meat quality characteristics. Genetic correlations between lean meat percentage and meat quality characteristics shown in Table 2-11 are in agreement with these findings from Hovenier et al. (1993). They show that a further increase in lean meat content will lead to inferior meat quality.

Table 2-11 Literature estimates of genetic (first row) and phenotypic correlations (second row) between carcass and meat quality traits

	N	Breed ¹	pH45	pH24	Colour	DLP	IMF	Cook loss
Backfat								
Cole et al. (1988)	8867	LW		0.20	-0.10	0.10 ⁴		
Cole et al. (1988)	4098	LR		-0.22	-0.13	0.07 ⁴		
Cole et al. (1988)	2840	B-LR		-0.10		-0.06 ⁴		
Cameron (1990b)	320	pooled		0.19	-0.48		0.05	
				0.13	-0.16		0.22	
Hovenier et al. (1992)	1113	pooled		0.15	0.00	-0.07	0.37	
				0.01	0.00	-0.03	0.30	
Lo et al. (1992)	960	pooled					0.60 ²	
							0.10	
Lo et al. (1992)	960	pooled					0.41	
							0.25	
Bidanel et al. (1994a)	1276	P	0.26	0.22		-0.20		-0.04
			0.00	0.03		-0.01		-0.06
Goodwin (1995)	2111	pooled		0.00	0.05			0.32
Lean meat percentage								
Lundeheim et al. (1980) ³	11292	pooled			0.13			
					0.14			
Johansson (1987b) ³	8234	LR		-0.09	0.21			
				0.04	0.09			
Johansson (1987b) ³	4448	Y		0.16	0.37			
				-0.36	-0.05			
Cole et al. (1988)	8867	LW		-0.09	0.17	-0.14 ⁴		
Cole et al. (1988)	4098	LR		-0.05	0.24	-0.37 ⁴		
Cole et al. (1988)	2840	B-LR		-0.09		-0.38 ⁴		
Hovenier et al. (1992)	1113	pooled		-0.11	0.17	0.11	-0.44	
				-0.04	0.01	0.11	-0.31	
de Vries et al. (1994b)	4055	Y	0.10	-0.07	-0.16	-0.10	-0.37	-0.06
			-0.01	-0.04	-0.03	0.05	-0.23	0.10
Loin eye area								
Malmfors and Nilsson (1979)	1212	LR			0.05			-0.34
					0.24			-0.16
Malmfors and Nilsson (1979)	978	Y			0.49	0.63	0.78	0.06
					0.17	-0.19	0.28	-0.11
Lundeheim et al. (1980)	11292	pooled			0.14			
					0.16			
Lo et al. (1992)	960	pooled					-0.40	
							-0.22	
Lo et al. (1992)	960	pooled					-0.31 ²	
							-0.06	
Goodwin (1995)	2111	pooled		-0.02	0.12			-0.37
Ham weight								
Johansson et al. (1987b) ³	8234	LR			0.27			
					0.04			
Johansson et al. (1987b) ³	4448	Y			0.29			
					-0.02			

¹ for breed abbreviations see Table 2-3; ² real time ultrasound; ³ restricted feeding regime; ⁴ water holding capacity

Only a few studies analysed genetic and phenotypic relationships between additional processing traits like eye muscle area and ham weight and meat quality characteristics (Table 2-11). The range of genetic correlations between colour and eye muscle area lies between 0.12 and 0.49, showing a moderate relationship of larger eye muscle area with paler meat. A large eye muscle area is also associated with a higher drip loss percentage and a reduced intramuscular fat content. However, genetic correlations between eye muscle area and cooking loss tend to be favourable with values ranging between -0.37 and 0.06. Johansson et al. (1987b) found a positive and therefore undesirable genetic correlation between ham weight and colour.

2.2.6 Reproductive traits of the sow

The reproductive performance of the sow is mostly described through litter size. Studies summarizing literature estimates of heritabilities for number born alive concluded that the heritability of litter size is around 0.09 (Haley et al., 1988) and 0.07 (Lamberson, 1990). Recent estimates of heritabilities for litter size found in the literature are presented in Table 2-12. The mean of heritability estimates is 0.07 for repeated records and 0.10, 0.11 and 0.10 for heritability estimates for the first, second and third parity. In comparison with other breeds, Iberian pigs, a local Spanish breed, show a low heritability with an average value of 0.05. Studies on Yorkshire populations found higher heritabilities for litter size (0.15). The highest heritability estimate of 0.33 for litter size was obtained from a selection experiment in a research herd (Rydhmer et al., 1992) with low number of observations and can partly be explained by a reduced environmental variation due to a better controlled management. Estimates of heritabilities show greater differences between studies for Landrace, indicating that this breed is more heterogenous between countries. In addition, Southwood and Kennedy (1990) found an influence of maternal effects for litter size in Landrace pigs leading to a higher heritability when maternal effects were fitted in the model.

Haley et al. (1988) suggested the use of repeated records of litter size in evaluation programs. This assumes genetic correlations of one between parities, which might not always be the case as Table 2-13 shows. Genetic correlations of litter size recorded in different parities were between 0.91 and 0.99 when analysed in bivariate analyses but dropped to 0.55 and 0.79 in a multivariate analysis incorporating the first five parities (Alfonso et al., 1994). In addition, Roehe and Kennedy (1995) and Rydhmer et al. (1995) found genetic correlations of 0.49 and 0.7 in Yorkshire pigs between litter size recorded in the first parity and litter size recorded in the second parity. These results are in agreement with an Australian study (Tholen et al., 1996b) which included Large White and Landrace pigs and a Synthetic line consisting of these

two breeds. Tholen et al. (1996b) found genetic correlations significantly different from one between number born alive in the first parity and later parities.

Table 2-12 Literature estimates of heritabilities (h^2) and repeatabilities (r) for litter size

Reference	N	Breed ¹	h^2	r	h^2 for parity:		
					1	2	3
Kaplon et al. (1991)	18683	LW	0.07	0.06			
Mercer and Crump (1990)	1891	LR	0.09	0.19			
Southwood and Kennedy (1990)	6068	LR			0.18		
Perez-Enciso & Gianola, (1992)	3655	Iberian	0.04				
Rydhmer et al. (1992)	393	Y			0.33		
Irgang et al. (1994)	1817	Duroc			0.15	0.11	0.10
Rodriguez et al. (1994)	2227	Iberian	0.06				
Siewerdt et al. (1995)	787	Duroc	0.07	0.15 ²			
Alfonso et al. (1994)	10194	LR			0.04	0.05	0.05
Irgang et al. (1994)	5799	LR			0.15	0.20	0.02
Roehe and Kennedy (1995)	16306	LR			0.09	0.10	0.11
Siewerdt et al. (1995)	1236	LR	0.12	0.16 ²			
Southwood and Kennedy (1990)	4307	Y			0.10		
Irgang et al. (1994)	4561	LW			0.09	0.15	0.18
Rydhmer et al. (1994)	4068	Y			0.13	0.12	
Roehe and Kennedy (1995)	11782	Y			0.10	0.09	0.14
Siewerdt et al. (1995)	2061	LW	0.06	0.14 ¹			
Tholen et al. (1996b)	3943	LR/LW			0.12	0.13	0.16
Tholen et al (1996b)	6050	LR/LW			0.10	0.11	0.09
weighted mean (according to N)			0.07	0.08	0.10	0.11	0.10

¹ for breed abbreviations see Table 2-3; ² Siewerdt and Cardellino (1995)

Literature values for heritabilities and repeatabilities for litter birth weight and average piglet weight at birth are presented in Table 2-14. Heritabilities for litter birth weight range from 0.10 to 0.54 with the tendency of higher estimates obtained from data collected in research herds. The mean of heritabilities for litter birth weight is 0.20 with a mean repeatability estimate of 0.18. Estimates of heritabilities for average piglet weight at birth obtained from research herds are higher than estimates obtained from field data with values of 0.64 and 0.45 (Irvin and Swiger, 1984; Rydhmer et al., 1992). These estimates are the in range of 0.19 to 0.35 (Mercer

and Crump, 1990; Tholen et al., 1996b). Litter birth weight and average piglet weight at birth are influenced by the milk intake of the piglet after birth which is dependent on the milk performance of the sow. It is therefore important to weigh piglets immediately after birth (Rydhmer et al., 1992) and later recording of piglets especially after cross fostering leads to an increase in environmental variation (Tholen et al. 1996b) with the consequence of a reduced heritability.

Table 2-13 Literature estimates of genetic (**above diagonal**) and environmental correlations (below diagonal) between number born alive in the first three parities ($NBA_{1,2,3}$)

	Breed	NBA₁	NBA₂	NBA₃
NBA₁				
Alfonso et al. (1994)	Landrace ¹		0.92	0.91
Alfonso et al. (1994)	Landrace ²		0.74	0.55
Roehe and Kennedy (1995)	Yorkshire		0.49	0.98
Roehe and Kennedy (1995)	Landrace		0.92	0.92
Rydhmer et al. (1995)	Yorkshire		0.7	
Tholen et al. (1996b)	Synthetic		0.74	0.74
Tholen et al. (1996b)	Large White /Landrace		0.56	0.57
NBA₂				
Alfonso et al. (1994)	Landrace ¹	0.14		0.99
Alfonso et al. (1994)	Landrace ²	0.14		0.55
Roehe and Kennedy (1995)	Yorkshire	0.12		0.66
Roehe and Kennedy (1995)	Landrace	0.07		0.99
Tholen et al. (1996b)	Synthetic	0.17		1.00
Tholen et al. (1996b)	Large White /Landrace	0.17		1.00
NBA₃				
Alfonso et al. (1994)	Landrace ¹	0.11	0.12	
Roehe and Kennedy (1995)	Yorkshire	0.06	0.14	
Roehe and Kennedy (1995)	Landrace	0.06	0.07	
Tholen et al. (1996b)	Synthetic	0.19	0.23	
Tholen et al. (1996b)	Large White /Landrace	0.14	0.22	

¹ bivariate analyses; ² multivariate analysis

Estimates of heritabilities for 21 day litter weight and average piglet weight are higher from research herds than field data (Table 2-15) ranging from 0.17 to 0.38 for studies analysing research data and ranging from 0.03 to 0.17 for estimates obtained from field data sets. These traits are strongly influenced by the number of piglets in the litter and the age of the litter when this trait is recorded (Tholen et al., 1996b). In many commercial herds crossfostering is a

common practice leading to a higher environmental variation which cannot be explained by the model in the analysis.

Table 2-14 Literature estimates of heritabilities (h^2) and repeatabilities (r) for litter birth weight (LBW) and average piglet birth weight (ABW)

Reference	data source ²	N	Breed ¹	h^2	r	h^2 for parity		
						1.	2.	3.
Litter birth weight								
Young et al. (1978)	R	2095	pooled	0.29				
Bereskin (1984)	R	999	pooled	0.10				
Irvin and Swiger (1984)	R	609	pooled	0.54				
Ferguson et al. (1985)	R	460	Duroc	0.21	0.14			
Ferguson et al. (1985)	R	663	Y	0.42	0.27			
Gu et al. (1989)	F	1018	pooled	0.12				
Mercer and Crump (1990)	F	1891	LR	0.13	0.22	0.11		
Siewerdt et al. (1995)	F	1236	LR	0.16	0.19 ³			
Siewerdt et al. (1995)	F	2061	LW	0.15	0.15 ³			
Siewerdt et al. (1995)	F	787	Duroc	0.11	0.13 ³			
weighted mean (according to N)				0.20	0.18			
Average piglet weight at birth								
Ferguson et al. (1985)	R	460	Duroc		0.38			
Ferguson et al. (1985)	R	663	Y	0.53	0.32			
Irvin and Swiger (1990)	R	609	pooled	0.65				
Tholen et al. (1996b)	F	4437	pooled			0.15	0.11	0.14
Tholen et al. (1996b)	F	3943	pooled			0.30	0.28	0.35
Mercer and Crump (1990)	F	1891	LR	0.21	0.28	0.19		
Rydhmer et al. (1992)	R	393	Y			0.45		
weighted mean (according to N)				0.36	0.30	0.22	0.19	0.24

¹ for breed abbreviations see Table 2-3; ² R: research herd, F: field data;

³ Siewerdt and Cardellino (1995)

Table 2-15 Literature estimates of heritabilities (h^2) and repeatabilities (r) for 21 day litter weight

Reference	data source ²	N	Breed ¹	h^2	r	h^2 for parity:		
						1	2	3
Young et al. (1978)	R	2095	pooled	0.38				
Bereskin (1984)	R	999	pooled	0.20				
Irvin and Swiger, (1984)	R	509	pooled	0.17				
Tholen et al. (1996b)	F	3943	pooled			0.17	0.12	0.23
Irgang et al. (1994)	F	5799	LR			0.15	0.17	0.03
Siewerdt et al. (1995)	F	1236	LR	0.14	0.15 ³			
Strang and King (1970)	F	38000	LW			0.14	0.03	0.05
Kaplon et al. (1990)	F	18683	LW	0.06	0.08			
Irgang et al. (1994)	F	4561	LW			0.08	0.17	0.18
Siewerdt et al. (1995)	F	2061	LW	0.13	0.13 ³			
Ferguson et al. (1985)	R	460	Duroc	0.25	0.17			
Irgang et al. (1994)	F	1817	Duroc			0.14	0.11	0.06
Siewerdt et al. (1995a,b)	F	787	Duroc	0.17	0.16			
Ferguson et al. (1985)	R	663	Y	0.19	0.24			
weighted mean (according to N)				0.11	0.10	0.14	0.07	0.07

¹ for breed abbreviations see Table 2-3; ² R: research herd, F: field data;

³ Siewerdt and Cardellino (1995)

Estimates of repeatabilities for the shown reproductive traits of the sow are only slightly higher than the estimated heritabilities. The repeatability expresses the proportion of the variance that is due to permanent differences between individuals and includes genetic and environmental effects (Falconer, 1989). The low estimates of repeatabilities show that temporary environment effects influence reproductive traits in different parities. By definition, the repeatability is never lower than the heritability. In this respect, heritability and repeatability estimates of Ferguson (1985), who found lower repeatability estimates than heritability estimates, have to be looked at with caution.

Table 2-16 summarizes genetic and phenotypic correlations between various reproduction traits. Number born alive has positive genetic and phenotypic correlations with litter birth weight and 21 day litter weight. Litter weight at birth and 21 days are dependent on the number of piglets in the litter resulting in these positive correlations. In contrast to the total litter weight, the individual weight of the piglet at birth is reduced with increasing litter size

which is shown through genetic correlations of -0.45 to 0.05. Tholen et al. (1996b) included 21 day litter weight in the analysis which was adjusted for the number of piglets at weighing. The average estimate of genetic correlation between litter size and 21 day litter weight for different parities (first to third) was -0.27. By adjusting 21 day litter weight in this way this trait is more similar to the average piglet weight at 21 days. This shows that the unfavourable relationship between litter size and average piglet weight is present not only at birth but also at 21 days.

Table 2-16 Literature estimates of genetic (**above diagonal**) and phenotypic (below diagonal) correlations between reproduction traits

References	N	Breed ¹	NBA	LBW	ABW	LW21
Number born alive (NBA)						
Strang and King (1970)	38000	LW				<i>0.80</i>
Young et al. (1978)	2095	pooled		<i>0.92</i>		<i>0.56</i>
Bereskin (1984)	999	pooled		<i>0.42</i>		<i>0.75</i>
Irvin and Swiger (1984)	601	pooled		<i>0.58</i>	<i>0.05</i>	<i>0.91</i>
Kaplon et al. (1990)	18683	LW				<i>0.68</i>
Rydhmer et al. (1992)	393	Y			<i>-0.34</i>	
Siewerdt et al. (1995)	2061	LW		<i>0.70</i>		<i>0.56</i>
Siewerdt et al. (1995)	1236	LR		<i>0.82</i>		<i>0.89</i>
Siewerdt et al. (1995)	787	Duroc		<i>0.59</i>		<i>0.37</i>
Tholen et al. (1996b)	3943	pooled			<i>-0.43</i>	
Tholen et al. (1996b)	6050	pooled			<i>-0.45</i>	
Litter birth weight (LBW)						
Young et al. (1978)	2095	LW	0.84			0.95
Bereskin (1984)	999	pooled	0.85			
Irvin and Swiger (1984)	601	pooled	0.77		0.76	0.88
Siewerdt et al. (1995)	2061	LW	0.88			0.74
Siewerdt et al. (1995)	1236	LR	0.89			0.83
Siewerdt et al. (1995)	787	Duroc	0.89			0.42
average piglet weight at birth (ABW)						
Irvin and Swiger (1984)	601	pooled	-0.35	0.14		0.40
Yen et al. (1987)	10976	pooled	-0.25			
Rydhmer et al. (1992)	393	Y	-0.10			
Tholen et al. (1996b)	3943	pooled	-0.22			0.39
Tholen et al. (1996b)	6050	pooled	-0.28			
21 day litter weight (LW21)						
Strang and King (1970)	38000	LW	0.5			
Young et al. (1978)	2095	LW	0.71	0.91		
Bereskin (1984)	999	pooled	0.55			
Irvin and Swiger (1984)	601	pooled	0.50	0.56	0.16	
Kaplon et al. (1990)	13683	LW	0.75			
Siewerdt et al. (1995)	2061	LW	0.75	0.78		
Siewerdt et al. (1995)	1236	LR	0.79	0.80		
Siewerdt et al. (1995)	787	Duroc	0.70	0.72		

¹ for breed abbreviations see Table 2-3

Genetic and phenotypic correlations between the three reproductive traits, litter birth weight, average piglet weight at birth and 21 day litter weight, are positive. The range for these genetic correlations is 0.39 to 0.95. Especially the high magnitude of genetic correlation between litter birth weight and 21 day litter weight suggests that 21 day litter weight could indirectly be improved through selection for litter weight at birth. This might be of advantage since cross fostering - a common practice in many herds could bias 21 day litter weight.

2.2.7 Reproductive traits of the sow and growth and carcass traits

Information on genetic relationships between reproduction traits and growth and carcass performance can be obtained in two ways. Genetic correlations can be estimated from family relationships and a summary of estimates is given in Table 2-17. These estimates of genetic parameters are often based on data from research herds with high standard errors and correlated response in reproductive performance from selection experiments might give additional information. These selection experiments are mostly based on growth rate and backfat and correlated response in reproduction performance gives an indication about genetic associations between the traits selected for and reproductive performance traits.

Genetic correlations between reproduction and performance traits presented in Table 2-17 are not consistent between studies. The majority of studies found genetic correlations between number born alive in the first parity and growth rate which are close to zero or slightly negative. In contrast, genetic correlations appear to be slightly positive between growth rate and litter size recorded in the second or later parities. However, genetic correlations between growth rate and litter weight traits at birth and at 21 days are consistently positive between studies, varying from 0.09 to 0.80.

Short et al. (1994) examined the genetic association between daily feed intake and number born alive for four PIC lines in the US. Although the genetic correlation between these two traits was 0.17 for one line, the other three lines have consistent negative genetic correlations ranging from -0.02 to -0.22. On average this indicates that a larger litter size is lowly correlated with a reduced feed intake. Morris (1975) estimated genetic relationships between food conversion ratio and number born alive from data originating from performance of boars and performance of siblings consisting of a castrate male and a female. However, these results differ between data sets with estimates ranging from -0.46 to 0.49.

Table 2-17 Literature estimates of genetic correlations between performance and carcass traits and reproductive traits

References	N	Breed ³	NBA gilts	NBA	BW	ABW	LW21
Average daily gain							
Morris (1975)	15704	LW	0.16 ¹	-0.02 ¹			0.13
			-0.07 ²	0.15 ²			
Morris (1975)	8222	LR	-0.15 ¹	0.44 ¹			0.77
			0.42 ²	1.25 ²			
Young et al. (1978)	2095	pooled		0.41	0.80		0.09
Vangen, (1980)	2150	pooled		-0.07		0.44	
Hutchens et al. (1981)	737	pooled				0.50	
Rydhmer et al. (1992)	393	Y		-0.14		0.41	
Short et al. (1994)	18643	PIC		0.04			
Short et al. (1994)	23307	PIC		0.23			
Short et al. (1994)	26848	PIC		-0.15			
Short et al. (1994)	27623	PIC		0.05			
Merks and Molendijk (1995)	32811	LR	-0.03				
Rydhmer et al. (1995)	4068	Y	-0.01				
Tholen et al. (1996b)	3943	pooled	0.07	-0.10		0.23	0.13
Tholen et al. (1996b)	6050	pooled	-0.11	0.11		0.27	
Daily feed intake							
Short et al. (1994)	6152	PIC		0.17			
Short et al. (1994)	9812	PIC		-0.12			
Short et al. (1994)	10729	PIC		-0.02			
Short et al. (1994)	27623	PIC		-0.22			
Food conversion ratio							
Morris (1975)	15704	LW	-0.31 ¹	0.20 ¹			-0.09
			-0.11 ²	-0.46 ²			
Morris (1975)	8222	LR	0.15 ¹	0.49 ¹			-0.40
			-0.04 ²	-0.46 ²			
Backfat							
Young et al. (1978)	2095	pooled		0.09	-0.05		0.14
Vangen, (1980)	2150	pooled		-0.21		-0.17	
Hutchens et al. (1981)	737	pooled				0.19	
Johansson and Kennedy (1983)	7275	LR	0.13	-0.05			
Johansson and Kennedy (1983)	3797	Y	0.22	0.13			
Short et al. (1994)	18643	PIC		-0.13			
Short et al. (1994)	23307	PIC		-0.03			
Short et al. (1994)	26848	PIC		0.06			
Short et al. (1994)	27623	PIC		-0.08			
Merks and Molendijk (1995)	32811	LR	0.06				
Rydhmer et al. (1995)	4068	Y	-0.11				
Tholen et al. (1996b)	3943	pooled	-0.06	0.04		-0.09	-0.10
Tholen et al. (1996b)	6050	pooled	0.22	0.26		-0.15	
Lean meat percentage							
Rydhmer et al. (1992)	393	Y	0.20			0.14	
Eye muscle area							
Morris (1975)	15704	LW	0.12 ²	-0.11 ²			
Morris (1975)	8222	LR	0.06 ²	-0.43 ²			

¹ based on testing of boars; ² based on testing of siblings (castrate male and female pair);

³ for breed abbreviations see Table 2-3

Genetic relationships between backfat and number born alive also seem to differ between the first and later parities. Estimates are mostly positive for the first parity, while estimates tend to be slightly negative for later parities. Estimates range from 0.19 to -0.17 between backfat and litter weight traits giving no clear picture about the relationship between these characteristics. Additionally, genetic correlations between lean meat percentage and eye muscle area are only based on one study in each case. Both carcass traits are positively correlated with number born alive in the first litter in contrast to negative genetic correlations found for the second parity (Morris, 1975). However, genetic relationships to litter weight traits have a positive magnitude (0.04 to 0.24).

So far, information about genetic correlations between reproduction traits and other performance traits is limited and correlated response in reproductive performance from selection for growth performance might give further information. Some results from recent selection studies are therefore summarized in Table 2-18. The Canadian study of Freeden and Mikami (1986) included replicate selection for growth rate, backfat and an index including both characteristics. Piglets were born in two seasons, season one including mid January to March and season two ranging from end of June to mid August. Correlated responses in reproductive traits were reported for both seasons. Only season one showed significant correlated responses for number born alive and litter weights at birth and at weaning. Selection for growth rate led to a decrease in number born alive and litter weight at birth, while litter weight at weaning was increased for this line. No significant correlated response was found for the line that was selected for a reduced backfat. All reproductive traits were improved for index line with selection being based on growth rate and backfat.

Correlated responses in reproductive traits were reported by Cleveland et al. (1988) from a selection experiment conducted at the University of Nebraska. The index practised over six generations included average daily gain and backfat with more emphasis being put on average daily gain than backfat. Cleveland et al. (1988) presented regression coefficients of line differences on cumulative selection differentials of the index. These regression coefficients were negative for number born alive and number weaned, and positive for litter weight at birth and weaning weight. However, none of these regression coefficients was significant relative to standard errors adjusted for genetic drift variance. It was suggested that index selection for lean growth should have little effect on litter size and litter weight.

A Canadian selection experiment applied six generations of selection for increased average daily gain and decreased backfat (McKay, 1990). The main emphasis was placed on backfat rather than increasing average daily gain. Correlated responses in litter size and 21 day litter

weight were analysed but no significant trend in these traits was found. It was therefore suggested that this index selection did not have a detrimental effect on the gilt's reproductive performance.

Kuhlers and Jungst (1992) described a selection experiment which selected pigs for an increased weight at 70 days of age. Only litter size at 21 days showed a significant correlated response of 0.24 piglets per generation, but litter size born alive and litter birth weight were not significantly influenced by selection for increased weight at 70 days. There was, however, the tendency for reduced reproduction performance in number born alive and litter birth weight, while litter weight at 21 days was improved slightly.

Table 2-18 Correlated response in reproductive performance from selection experiments

Reference	Selection Criteria	N. of generations	correlated response per generation for:			
			NBA	ABW	LBW	LW21
Freeden and Mikami (1986)	growth rate	9	-0.11		-0.16	
Freeden and Mikami (1986)	index of growth rate and backfat	9	0.11		0.29	3.81
Woltmann (1993) ³	growth rate:	5				
	ad libitum feeding				-0.446	-2.09
	restricted feeding		-0.082	-0.016	-0.273	-1.06
Kerr and Cameron (1995)	daily food intake	5	0.08 ¹	-0.026 ¹	-0.01 ¹	-2.58 ¹
			-0.30 ²	-0.036 ²	-0.14 ²	-6.08 ²
Kerr and Cameron (1995)	lean food conversion	5	-0.32 ¹	-0.026 ¹	-0.40 ¹	-2.30 ¹
			-0.06 ²	-0.010 ²	-0.04 ²	1.16 ²

¹High line; ²Low line; ³ cited in Clutter (1995)

Growth rate in ad libitum feeding and restricted feeding was used as a selection criterion in an experiment undertaken at Oklahoma State University. Woltmann (1993) (cited in Clutter, 1995) reported a trend to negative correlated responses in litter size, litter weight and preweaning piglet weight for both selection lines. Although all reproductive traits showed a negative response, only changes in litter weight at birth and 21 days for the line selected for growth rate on ad libitum feeding were significant. Selection for growth rate led to a decrease of -0.446 kg generation for litter weight at birth and of -2.09 kg generation for 21 day litter weight (Table 2-18).

Kerr and Cameron (1995) studied correlated responses in reproductive performance to five generations of divergent selection for daily food intake, lean food conversion, growth rate on ad libitum feeding and growth rate on restricted feeding. No significant effect of selection for lean growth on either ad libitum feeding or restricted feeding on reproductive performance in gilts was found. However, selection for low daily food intake and high lean food conversion resulted in reduced reproductive performance

2.2.8 Conclusions

In this chapter heritabilities and genetic correlations from the literature were presented. In order to obtain an overview, mean heritabilities and genetic correlations are summarized in Table 2-19 for production, carcass and meat quality traits. Mean heritabilities from the literature range from 0.26 to 0.41 for performance traits while higher heritabilities are found for carcass traits. The range of average heritability estimates for these traits is 0.43 to 0.70. Genetic response for meat quality traits can be expected since mean estimates of heritabilities vary from 0.15 to 0.24. The average heritability estimate is higher for intramuscular fat content with a value of 0.45.

Genetic correlations between the main performance traits are high and well documented. In summary, a high growth rate is associated with a high feed intake and a reduced feed conversion ratio. In contrast, feed intake has an unfavourable relationship with feed conversion ratio; a high feed intake will lead to a higher feed conversion ratio. Many studies estimated genetic correlations between growth rate and backfat or lean meat percentage. In ad libitum feed systems, a higher growth rate is associated with a higher backfat and a reduced lean meat percentage. This relationship is of opposite sign in restricted feeding systems which have an average genetic correlation between growth rate and lean meat percentage of 0.35 (not shown in Table 2-19). Estimates of genetic correlations between performance traits and meat quality traits are sparse. Average values of genetic correlations between performance traits and pH measurements are not significantly different from zero. However, a high growth rate is related to a paler meat and an increased drip loss percentage (r_g : 0.25 for colour and -0.18 for drip loss percentage).

Generally, carcass traits are highly correlated with each other. The known relationship of inferior meat quality for lean pigs seems to have weakened in more recent studies. This might be due to the reduction of the halothane gene in these populations.

Table 2-19 Mean literature estimates of heritabilities (on diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for production, carcass and meat quality traits with number of studies (in brackets)

	ADGT	FDINT	FCR	LEANG	BF	LOIN	LEAN	HAM	PH45	pH24	COL	DLP	COOK	IMF
ADGT	0.35 (19)	0.69 (7)	-0.43 (7)	0.87 (6)	0.25 (14)	-0.16 (2)	-0.18 (3)	-0.08 (6)	0.05 (2)	-0.01 (8)	0.25 (8)	0.18 (4)	-0.05 (1)	0.10 (7)
FDINT	0.69 (5)	0.36 (8)	0.42 (4)	0.16 (1)	0.40 (4)	-0.48 (1)	-0.48 (1)	-0.72 (1)	-0.02 (2)	0.12 (2)	-0.12 (2)	-0.35 (1)	-0.10 (1)	0.21 (2)
FCR	-0.44 (6)	0.31 (4)	0.26 (10)	-0.87 (2)	0.25 (4)	-0.19 (1)	-0.38 (5)	-0.52 (2)	-0.14 (1)	-0.04 (1)	-0.12 (2)			0.10 (4)
LEANG	0.77 (2)	0.22 (1)	-0.82 (2)	0.41 (6)	0.02 (1)	0.47 (1)	0.81 (3)		0.14 (1)					
BF	0.22 (11)	0.34 (4)	0.12 (4)	0.11 (1)	0.43 (26)	-0.50 (4)	-0.84 (3)	-0.58 (4)	0.26 (1)	0.05 (7)	-0.09 (5)	-0.07 (5)	0.18 (2)	0.42 (4)
LOIN	0.05 (2)	-0.21 (3)	-0.16 (1)	0.40 (1)	-0.38 (4)	0.51 (5)	0.66 (1)	0.66 (1)	-0.02 (4)	-0.02 (7)	0.14 (4)	0.63 (1)	-0.16 (2)	0.03 (3)
LEAN	-0.21 (3)	-0.42 (1)	-0.14 (3)	0.34 (3)	-0.79 (3)	0.66 (1)	0.70 (8)	0.46 (2)	0.10 (1)	-0.05 (7)	0.16 (7)	0.17 (5)	-0.06 (1)	-0.39 (2)
HAM	-0.14 (4)	-0.62 (1)	-0.37 (2)		-0.24 (2)	0.52 (2)	0.44 (9)		0.28 (2)					
pH45	0.02 (2)	0.04 (1)			0.00 (1)	-0.01 (1)			0.20 (3)	0.28 (4)	-0.59 (3)	-0.32 (2)	-0.32 (2)	0.25 (2)
pH24	0.02 (4)	0.12 (1)			0.03 (3)	-0.08 (4)			0.16 (4)	0.17 (8)	-0.33 (10)	-0.52 (6)	-0.77 (2)	0.11 (5)
Colour	0.06 (5)	-0.05 (2)	-0.11 (1)	0.12 (1)	-0.04 (2)	0.17 (3)	0.07 (5)	0.02 (2)	-0.39 (3)	-0.24 (10)	0.24 (5)	0.67 (5)	0.40 (2)	-0.08 (5)
DLP	-0.03 (1)	-0.11 (1)			-0.02 (2)	-0.19 (1)	0.06 (2)		-0.26 (2)	-0.29 (3)	-0.42 (6)	0.17 (2)	0.63 (3)	-0.15 (2)
COOK	-0.10 (1)	-0.12 (1)			0.22 (4)	-0.14 (2)	-0.25 (2)		-0.10 (2)	-0.36 (2)	0.32 (1)	0.31 (3)	0.15 (4)	-0.03 (1)
IMF	0.14 (6)	0.20 (2)	0.14 (4)		-0.06 (1)	0.00 (3)	0.10 (1)		0.10 (2)	0.04 (4)	0.03 (4)	-0.03 (2)	-0.09 (1)	0.45 (8)

Genetic correlations between meat quality traits reflect characteristics of PSE and DFD meat. The magnitude of these genetic correlations ranges from 0.28 to 0.77. The importance of intramuscular fat content arises from its favourable relationships to palatability traits. However, it also is favourably correlated with meat quality traits describing PSE and DFD meat, showing that a higher intramuscular fat content will reduce the incidence of PSE.

A summary of genetic parameters for reproduction traits is given in Table 2-20 while Table 2-21 provides an overview of genetic correlations between reproductive traits of the sow and other important performance traits. A large litter size is strongly correlated with a high litter birth weight and 21 day litter weight. However, breeding programs have to consider the negative relationship between number born alive and average piglet weight at birth. Weight traits consisting of litter birth weight, average piglet weight at birth and 21 day litter weight are highly correlated with each other.

Table 2-20 Mean literature estimates of genetic (**above diagonal**) and phenotypic (below diagonal) correlations between reproduction traits with number of studies (in brackets)

	NBA	LBW	ABW	LW21
Number born alive (NBA)		0.72 (6)	-0.41 (4)	0.61 (10)
Litter birth weight (LBW)	0.86 (6)		0.76 (1)	0.79 (5)
Average piglet weight at birth (ABW)	-0.24 (3)	0.14 (1)		0.40 (1)
21 day litter weight (LW21)	0.59 (8)	0.80 (5)	0.16 (1)	

Information about genetic correlations between reproductive traits of the sow and other performance traits is based on a few studies (Table 2-21). Genetic correlations between number born alive and other traits are low ranging from -0.12 to 0.20. In contrast, litter birth weight, average piglet weight at birth and 21 day litter weight are positively correlated with growth rate. This shows that these weight traits are to some extent dependent on the growth potential of the animal. Interestingly, these weight traits have favourable relationships to backfat although estimates are of low magnitude.

Table 2-21 Mean literature estimates of genetic correlations between reproduction and other performance traits with number of studies (in brackets)

	ADG	FDINT	FCR	BF	LEAN
NBA₁	-0.02 (8)		-0.12 (4)	0.08 (6)	0.20 (1)
NBA	0.14 (13)	-0.12 (4)	-0.08 (4)	-0.02 (10)	
LBW	0.80 (1)			-0.05 (1)	
ABW	0.30 (5)			-0.12 (4)	0.14 (1)
LW21	0.30 (5)		-0.19 (2)	-0.02 (2)	

In this chapter, heritabilities and genetic correlations from the literature were briefly summarized. This will be the basis for comparisons between estimates obtained in this study and literature estimates.