Genetic aspects of feed intake in lactating sows

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Abstract

Productivity of sows has increased worldwide, especially during the last decade. Sows have been changed genetically to produce larger litters. It was hypothesized that including feed intake or feed efficiency during lactation or both in the breeding objective for dam lines is necessary to facilitate sow's future increase of unproblematic production of grower-finishers that efficiently convert feed into meat. Increasing feed intake of sows is one solution to prevent excessive mobilization from body stores. As a result of selection for leaner pigs with higher feed efficiency, however, feed intake tends to decrease because high leanness and high feed efficiency are genetically associated with low appetite. There is a risk, therefore, that feed intake during lactation reduces due to selection for lean and efficient finishing pigs.

In this thesis a model was developed to estimate the energy efficiency of a lactating sow based on on farm observations enabling large scale data recording. Increasing energy efficiency during lactation might be a solution to overcome the apparent contradiction of the desired direction of selection for feed intake during growing-finishing and lactation. Increased energy efficiency during lactation will yield more milk output given the feed intake and mobilization from body stores.

To study the consequences of selection, heritabilities and genetic correlations were estimated for fertility, lactation performance and growing-finishing characteristics. For growing-finishing characteristics the genetic models contained social interactions and for lactation feed intake, environmental sensitivity was studied as well.

The main conclusion of a simulation of a breeding program in pigs was that it is possible to achieve a balanced genetic progress in fertility, lactation performance and growing-finishing characteristics. Genetic regulation of feed intake during growing-finishing is to a large extend different from genetic regulation of feed intake during lactation. Results of this thesis show that feed intake of sows during lactation is not an immediate risk for further improvement of more and heavier piglets. Higher piglet production is still on its way via the genetic pipeline and will continue to increase by selection for more and heavier piglets. Selection for increased milk production or litter weight gain is preferred; this will lead to increased protein and energy demands as well. At all events, sows need to eat more and be more efficient at the same time to keep up with this increased demand. It is a question of tuning the breeding objective in order to optimize the relation between feed intake and body weight losses during lactation.

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General introduction

1.1 Introduction

In commercial pig breeding programs the genetic lag between the nucleus herds and the commercial population is five to ten years. Because commercial pig breeding is a global activity, the effectiveness of a breeding program depends to a large extend on developments of the global markets in those five to ten years' time. Worldwide four major trends are very important for pig breeding companies.

1. Increased animal productivity. The future competitiveness of pork in the food market depends on continued genetic improvement in the efficiency of quality lean meat production (Clutter and Brascamp, 1998). Production levels of sows have increased continuously, especially during the last decade. Not only as a result of improved nutrition and husbandry but also as a result of breeding. In Table 1.1 sow productivity over the last 10 years in the USA is depicted. In order to stay competitive, commercial pig breeding programs will ensure increased production in the next decade too.

2. Decrease in availability of human labor per animal. An increasing share of livestock production will probably come from industrial enterprises. In recent years production from industrial enterprises has grown twice as fast as that from more traditional mixed farming systems (FAO 2002). Increased size of sow herds will also lead to more efficient animal production. This trend is depicted in Table 1.2 for pig husbandry in the Netherlands over the last 20 years. The amount of human labor available per animal, expressed in minutes per piglet sold was reduced by 60% in 20 years' time. Table 1.1 and Table 1.2 both demonstrate that the average size of sow herds has roughly doubled in the last 10 years.

3. Shift of production towards developing countries. Human diets in developing countries change as income rises. The share of staple food in human diets, such as cereals, roots and tubers, is declining, while that of meat, dairy products and oil crops is rising. Global production of meat is projected to more than double from 229 million tons in 1999 to 465 million tons in 2050, a growth predicted to be fastest in developing counties such as Latin America and South and East Asia (FAO 2006). Increase in production volume will predominantly happen in Latin America and South and East Asia because in developing countries, demand will grow faster than production. Because developing countries are often warmer, the demand for temperature tolerant pigs or robust pigs will increase. Knap (2005) defined robust pigs as "pigs that

Table 1.1 Development of sow productivity in the USA over the last ten years (PigCHAMP, 2010).

Trait	1999	2001	2003	2005	2007	2009
Average N^o of sows per farm	612	786	1046	1332	1319	1390
Total born per litter	11.1	11.3	11.4	11.9	12.3	12.8
Stillborn per litter	0.8	0.9	0.9	0.9	1.0	0.9
Pre-weaning mortality, %	12.4	13.8	13.4	12.2	12.3	12.2
Piglets weaned per litter	9.0	8.9	9.0	9.3	9.6	10.2
Piglets weaned per sow per year	19.6	19.7	20.2	21.8	22.2	23.4

combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions.".

4. Extra attention for reduction of ecological footprint in pig production. Environmental concerns are of major importance for the future. As emphasized by Kanis et al. (2005), the quantity of minerals (in particular N and P) and heavy metals excreted in manure per kilogram of meat produced largely depends on production and reproduction efficiencies. In particular, improving growth rate and feed efficiency have a favorable environmental impact. Kanis et al. (2005) even suggest putting more emphasis on these traits in the aggregate breeding objective than the weight they would have when based solely on their economic value. After years of decreasing feed usage on sow farms, expressed as the sum of feed used for sows and feed used for piglets per piglet sold, feed usage seem to increase again (Table 1.2). The increase since 2005 is entirely due to increased amount of feed fed to sows (results not shown).

Table 1.2 Development of working productivity and feed usage on sow farms in the Netherlands over the last 20 years (LEI, 2010).

Trait	1988	1993	1998	2003	2004	2005	2006	2007	2008[1]
Average N^o of sows per farm	178	185	232	328	339	374	402	401	427
N^o piglets sold per sow per year	19.2	20.6	21.1	22.7	22.8	24.1	25.7	24.9	26.6
Labor, minutes per piglet sold[2]	63	52	45	35	34	30	28	29	25
Weight of piglets sold, kg/piglet	25.3	24.7	25.9	25.7	25.3	24.8	24.9	25.8	24.3
Feed usage, kg feed[3]/kg piglets	3.51	3.31	3.11	3.18	3.11	3.03	3.24	3.44	3.52

[1] Preliminary results;
[2] Total annual labor used divided by number of pigs sold annually;
[3] Sum of feed for sows and piglets.

Future breeding objective
These global trends make that commercial breeding programs aim at high productive, self-supporting, robust animals that efficiently convert feed into meat. Feed intake plays a key role in this future breeding objective. Higher feed intake facilitates higher production. A high and continuous feed intake is a feature of self-supporting, robust animals. To reduce production costs and to reduce the ecological footprint of pig production, feed efficiency needs be improved too. Feed intake and feed efficiency of grower-finishers have been extensively subjected to research (Cameron and Curran, 1994; Dekkers and Gilbert, 2010). Feed intake and feed efficiency of sows, however, have got little attention. At present there is no common trait defined for efficiency of feed utilization in lactating sows in practice.

Effect of selection for growing-finishing traits on lactation feed intake and -efficiency
If feed intake capacity or feed efficiency of sows is considered, the lactation period is the most relevant phase. Lactation is a critical phase in life for piglets as well as for sows. A high and continuous feed intake of the sow during lactation ensures a good start of the productive life of piglets, a good prospect for the next cycle of the sow and a lower labor requirement for the farmer. Feed intake of sows during lactation is at present not high enough to sustain the milk production needed for large litters (Noblet et al., 1998; Eissen 2000); let alone for the production increases in the genetic pipelines. From a breeder's perspective, lactating sows should ideally have a high and continuous intake of feed which is efficiently converted to milk for her piglets.

As already mentioned, litter size will continue to increase in coming years. To support large litters, it is important to keep sows in proper body condition. If the increasing energy requirement cannot be met through extra feed intake, sows mobilize fat from body stores. Some mobilization of fat is not a problem, but excessive mobilization or, worse, mobilization of protein can result in fertility problems in the next farrowing cycle (Whittemore and Morgan, 1990; Clowes et al., 2003). Increasing feed intake of sows is one solution to prevent excessive mobilization of energy from body stores. As a result of selection for lean pigs with high feed efficiency, however, feed intake tends to decrease because high leanness and high feed efficiency are genetically associated with low appetite (Kanis, 1990). There is a risk, therefore, that feed intake during lactation will diminish due to selection for lean and efficient finishing pigs. This means that pig breeding programs face an important question: how to combine selection for mothering ability, amongst them milk production, with selection for efficient lean meat

production? Increasing energy efficiency during lactation might be a solution: more milk output given the feed intake and mobilization from body stores.

There are no widely used industry definitions to express the (energy) efficiency of the sow during lactation. Therefore, in this thesis such a trait will be developed and described, preferably based on 'on farm' observations which allow for large scale data collection. This trait will from now on be called lactation efficiency. Usefulness of including of lactation efficiency or its underlying traits (further on called lactation performance) in a breeding program depends on its heritability its economic value and its relationship with other traits of interest.

Body fat is an important energy store for sows and this can be efficiently mobilized during lactation (Noblet et al., 1990). Selection for higher feed efficiency in growing-finishing pigs will most probably make sows lean too and might, as a result, reduce feed intake during lactation and might reduce body mobilization because sows become lean genotypes. Reduced availability of energy will reduce milk yield and thus litter weight gain. Next to the expected negative effect of selection for growing-finishing traits on lactation feed intake, this example of leanness of sows shows that there might be a conflict in the desired selection for fertility- and grower-finishing traits.

Lacking knowledge

To optimize genetic selection for high productive, self-supporting, robust animals that efficiently convert feed into meat, heritabilities of lactation performance- , fertility- and growing-finishing traits and genetic correlations amongst these traits should be known. In addition, phenotypic correlations are needed to enlarge our knowledge of the biological backgrounds on which selection acts. With that, we might shine a bit of light on our black-box technique. Knowledge about the genetic regulation of traits as well as some biological backgrounds will offer the opportunity to understand, anticipate and prevent negative side effects of selection.

At present little is known about the heritability of lactation performance traits and the genetic and phenotypic correlations between lactation performance and fertility traits and between lactation performance and growing-finishing traits.

Recent developments

Social interactions among individuals are ubiquitous both in animals and plants, and in natural as well as domestic populations. These interactions affect both the direction and magnitude of responses to selection, and are a key factor in evolutionary success of species and in the design of breeding schemes in

agriculture. At present, however, very little is known of the contribution of social effects to heritable variance in trait values. Social interactions between pigs profoundly affect their welfare and performance because excessive aggression and oral manipulation of pen-mates, e.g. tail biting, can have detrimental effects, whereas affiliate relationships may enhance adaptability by offering 'social support'. If these social interactions become part of the breeding objective one might expect that animals spend less energy on fighting and stress and thus become more efficient. Adoption of this new methodology might change heritabilities and genetic correlations estimates.

If we only consider the robustness definition on sow feed intake, we are looking for sows that show a high feed intake during lactation no matter what the external stressors are. These animals need little management attention. A high and continuous feed intake during lactation is not obvious. For example, at commercial farms in the US, 38.3 % of the sows showed a major drop in feed intake (a decrease of ≥ 1.8 kg/d relative to the previous peak feeding level with remaining low feed intake for at least two days) during lactation (Koketsu et al., 1996). Models have shown that environmental sensitivity increased in response to selection for high productivity in a non-limiting environment (Kolmodin et al., 2003; Van der Waaij, 2004). Bloemhof et al. (2008) found a significant difference in heat tolerance between two purebred dam lines. One of the lines was a highly productive line, raised in nucleus herds with superior environments in a temperate environment. The other dam line was a less productive line predominantly raised in tropical environments. The high productive line showed a steep decrease in number of piglets per insemination when the insemination took place at temperatures above the upper critical temperature of sows. The dam line raised in the tropical environment showed no decline at these conditions. These results indicate that differences exist in regard to environmental sensitivity of sows which is one aspect of robustness in pigs. Genetic selection potentially offers opportunities to reduce environmental sensitivity.

Hypothesis and objectives of this thesis

It is hypothesized that including feed intake or feed efficiency during lactation or both in the breeding objective for dam lines is necessary to facilitate sow's future increase of unproblematic production of grower-finishers that efficiently convert feed into meat. The aims of this thesis that follow from the hypothesis are therefore:

1. Define feed efficiency of sows during lactation, based on 'on farm' observations.
2. Estimation of genetic parameters for feed efficiency of lactating sows and other lactation performance traits.
3. To investigate the relation between lactation performance and fertility traits and between lactation performance and growing-finishing traits. While analyzing growing finishing traits, recent developments on social interactions will be evaluated.
4. To evaluate the consequences of a traditional breeding program on the expected genetic response on lactation performance.
5. To make a next step towards defining robustness in lactating sows.
6. And finally the general discussion will address the possible physiological limits to genetic selection for lactation traits and evaluates the consequences of alternative breeding objectives.

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2

Lactation efficiency as a result of body composition dynamics and feed intake in sows

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Abstract

Through genetic selection and improvement of environment, litter size of sows increases. Increased energy requirement during lactation, increases the risk of excessive mobilization from body stores, with detrimental effects on reproductive performance. Feed intake capacity tends to decrease due to selection towards leaner pigs with a lower feed conversion ratio. However, to facilitate sows to wean large litters extra feed intake, or even better, a higher feed efficiency during lactation would be favourable. The objective of the present study was to describe the dynamics of body composition of sows and piglets during lactation, and to relate these traits to a newly introduced trait called "lactation efficiency". Energy metabolism of lactating sows was described, based on on-farm observations of weight and backfat of sows before parturition and at weaning, weight of piglets at birth and at weaning and feed intake of sows during lactation. "Lactation efficiency" was defined as energy efficiency of sows, and calculated for individual sows at two different farms. The average lactation efficiency was 68% and 65% for both farms; meaning that 68 and 65% of the metabolisable energy through feed intake or mobilization from body stores, above maintenance of the sow (input), was used for piglet growth and piglet maintenance (output). The association between lactation efficiency and other reproductive traits was studied by estimating the correlations within farms. Sows with a higher lactation efficiency showed lower feed intake ($r=-0.27$ and $r=-0.35$ for both farms respectively) and smaller fat losses ($r=-0.34$ and $r=-0.29$, respectively). The energy output of efficient sows was slightly higher ($r=0.23$ and $r=0.30$). The more efficient sows were the better mothers, as mortality of their piglets was lower ($r=-0.12$ and $r=-0.16$), piglet growth rate was higher ($r=0.16$ and $r=0.23$), and at weaning their litters were less variable ($r=-0.08$; only available at one farm). Results were remarkably similar for the two farms, despite different feeding strategies. Extra input, by means of feed intake or mobilization from body stores generated extra output by means of litter weight at weaning. This experiment demonstrated that an accurate recording of energy metabolism and relevant reproduction traits with little intervention is possible on commercial farms.

Key words: Sow Lactation, Energy efficiency, Body composition, Feed intake

2.1 Introduction

Productivity of sows has increased worldwide, especially during the last decade. Sows have been changed genetically to produce larger litters. The environment of sows, and herd management aspects such as feeding and health care have been improved too over the years. In the Netherlands, for example, the number of piglets per sow weaned each year increased from 23.0 in 2001 to 25.8 in 2007 (Kengetallenspiegel, 2002, 2008). Increased litter size accounted for the major part of this change. In 2007, the average number of live and stillborn piglets was 13.6 per litter. The number of litters per sow per year hardly changed over these years (2.34 in 2001 compared to 2.35 in 2007). Mortality of piglets from birth until weaning (litter mortality) increased from 11.8% in 2001 to 12.8% in 2007. Extrapolation of the trend in litter size will yield 15.8 live and stillborn piglets in 2017, assuming no other biological constraints. 15.8 live and stillborn piglets is a 28% increase compared to 12.3 live and stillborn piglets per litter in 2001.

To support large litters, it is important to keep sows in proper body condition. Feed intake of sows during lactation is often not high enough to sustain the milk production needed for large litters (Noblet et al., 1998; Eissen, 2000). If the increasing energy requirement cannot be met through extra feed intake, sows mobilize from body stores. Some mobilization of fat is not a problem, but excessive mobilization or, worse, mobilization of protein can result in fertility problems in the next farrowing cycle (Whittemore and Morgan, 1990; Clowes et al., 2003). Increasing feed intake of sows is one solution to prevent excessive mobilization from body stores. As a result of selection for leaner pigs with higher feed efficiency, however, feed intake tends to decrease because high leanness and high feed efficiency are genetically associated with low appetite (Kanis, 1990). There is a risk, therefore, that feed intake during lactation reduces due to selection for lean and efficient finishing pigs. This means that pig breeding programs face an important question: how to combine favourable mothering ability with favourable finishing characteristics? Increasing energy efficiency during lactation might be a solution: more milk output given the feed intake and mobilization from body stores.

The objective of this study was to describe the dynamics of body composition of sows and piglets during lactation, to introduce a new trait called "lactation efficiency", and to demonstrate the characteristics of "lactation efficiency".`

2.2 Materials and methods

Model

Energy metabolism of lactating sows can be described if the various energy sources of input and output are known. From this knowledge, the overall energy efficiency of a sow can be derived. The energy metabolism of lactating sows is depicted in Figure 2.1, which schematically shows the energy flow from input in sows to output through piglets. Feed intake and changes in body composition of sows and piglets are the major energy sources. Input is the amount of energy in feed after subtracting the amount of energy needed for maintenance of the sow, plus the amount of energy of mobilization from body stores of the sow. Sows provide energy to piglets through milk for growth and maintenance. Output thereby becomes the amount of energy deposited in fat and protein of piglets plus the amount of energy needed for the maintenance of the piglets.

In our study, all energy units were expressed in MJ Metabolisable Energy (ME). Input was calculated as:

Input, MJ ME/d = (energy from total feed intake during lactation   (1)
+ energy from body fat mobilization of the sow
+ energy from body protein mobilization of the sow
− energy needed for maintenance of the sow)
÷ lactation length.

Output during lactation was calculated as:

Output, MJ ME/d = (energy in fat deposition of live piglets at weaning   (2)
+ energy in protein deposition of live piglets at weaning
+ energy in fat deposition of dead piglets
+ energy in protein deposition of dead piglets
+ energy needed for maintenance of weaned piglets
+ energy used for maintenance of piglets that died before weaning)
÷ lactation length.

Lactation efficiency is defined as the energy efficiency of sows during lactation. The higher the lactation efficiency the more of the available energy (input) is used for piglet growth (output):

Lactation efficiency, % = output × 100 / input.   (3)
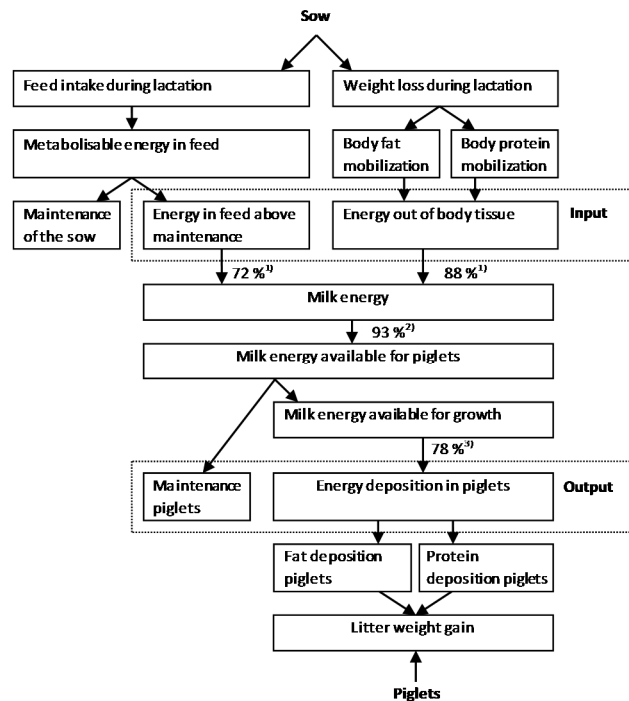
Figure 2.1 Schematic flowchart of the energy metabolism in lactating sows. [1] Noblet et al. (1990); [2] Everts et al. (1995); [3] Mullan et al. (1993).

Lactation efficiency is the overall efficiency. The specific efficiencies of various energy sources for milk syntheses or for piglet growth were ignored. Underlying components of input and output were based on on-farm observations of weight and backfat of sows before parturition and at weaning, weight of piglets at birth and at weaning and feed intake of sows during lactation. Equations are described in detail in the Appendix.

Sensitivity aspects of lactation efficiency

Table 2.1 demonstrates the sensitivity of lactation efficiency. Two possible sources of inaccuracy can be distinguished: the consequences of inaccuracy of formulas and the consequences of inaccuracy of observations. To demonstrate the consequences of inaccuracy of formulas, the effect of a 10% increase in each component of lactation efficiency on lactation efficiency is shown for a hypothetical sow, keeping all other components constant. To demonstrate the consequences of observation errors, each component was increased by 10% of its standard deviation. The hypothetical sow was of second parity, weighed 220 kg at transfer to the farrowing

Table 2.1 Sensitivity of Lactation Efficiency (LE); the consequences of inaccuracy of formulas and of observation errors of underlying traits (basis = hypothetical sow).

	Components of the lactation efficiency Model	Equation[1]	Basis	Basis +10%	LE_{new}	$LE_{new}-LE_{old}$[2]
Formulas[3]	Energy content of feed, MJ ME/kg		13.5	14.9	57.0	-5.8
	Protein losses of the sow during lactation, kg	(4)	2.2	2.4	62.6	-0.2
	Fat losses of the sow during lactation, kg	(5)	11.8	13.0	61.1	-1.7
	Weight adjustment at parturition, kg	(9)	20	22	63.3	+0.5
	Weight adjustment at weaning, kg	(10)	1.7	1.8	62.7	-0.1
	Maintenance of the sow, MJ ME/d	(12)	22.5	24.7	65.0	+2.2
	Maintenance of the piglets, MJ ME/d	(12)	14.2	15.6	65.0	+2.2
	Fat deposition of piglets until weaning, kg	(13)	11.0	12.1	65.4	+2.6
	Protein deposition of piglets until weaning, kg	(14)	10.3	11.4	64.3	+1.5
	Weight of dead piglets, kg	(16)	5.0	5.5	63.2	+0.4
Observations[4]	Weight at transfer to the farrowing house, kg		220	223.4	61.9	-0.9
	Backfat at transfer to the farrowing house, mm		17	17.4	61.8	-1.0
	Weight of living piglets after cross fostering, kg		18	18.3	63.0	+0.2
	Total feed intake of the sow during lactation, kg		125	128.0	61.3	-1.5
	Weaning weight sow, kg		180	183.5	64.1	+1.3
	Backfat at end of lactation, mm		12	12.4	63.8	+1.0
	Litter weight at weaning, kg		77.5	79.1	64.2	+1.4

[1] The equation number refers to the equations in the appendix;
[2] LE_{old} = Lactation efficiency of the hypothetical sow, before any changes (62.8%);
[3] The consequences of an increase by 10% of the specified trait;
[4] The consequences of an increase by 10% of the standard deviation of the specified trait.

house at day 108 of gestation, and had 17 mm backfat. She farrowed at 115 d of gestation 12 live born piglets at an average of 1.5 kg each, two of which died at 5 d of age. During 25 d of lactation, she consumed 125 kg of feed. At the end of her lactation, she weighed 180 kg, having 12 mm of backfat. The weaned piglets showed a growth rate of 250 g/d. The sow had a calculated input from feed and mobilization from body stores of 65.8 MJ ME/d. Her calculated output was 41.3 MJ ME/d. Output over input yields an energy efficiency of 62.8% (=LE_{old} in Table 2.1).

Lactation efficiency is most sensitive to errors in energy content of feed. Energy content of lactation feed was assumed at 13.5 MJ ME/kg. If this should be 14.9 MJ ME/kg, lactation efficiency becomes 57% instead of 62.8%, a difference of 5.8%. Applying Equation (4) once with start weight and again with end weight for the hypothetical sow would yield a protein loss during lactation of 2.2 kg. If the outcome should be 2.4 kg instead of 2.2 kg, lactation efficiency would hardly be affected (a 0.2% decrease). A 10% underestimation of the real fat losses of a sow

during lactation would change lactation efficiency by 1.7%. Errors in weight adjustment of the sow at parturition or at weaning are of minor importance to lactation efficiency (+0.5% and −0.1% respectively). Maintenance of the sow as well as her piglets was estimated by using Equation (12). A 10% underestimation would affect lactation efficiency by 2.2% in both situations. Fat and protein deposition during lactation of the 12 live born piglets of the hypothetical sow were estimated applying Equations (13) and (14). A 10% change of fat deposition has a higher impact on lactation efficiency (2.6%) than protein deposition (1.5%) has, because the energy content of fatty tissue is higher than that of protein. Under or overestimation of weight of piglets that died during lactation (Equation (16)) is of minor importance to lactation efficiency.

The effect of registration errors on lactation efficiency was more or less of the same magnitude for all observations, except for litter mass at birth. A difference of 0.3 kg litter mass (10% of the standard deviation) was of minor importance. When litter mass is higher extra energy is needed for maintenance of piglets. At the same time, calculated growth rate decreases and as a result energy deposition by piglets decreases. Registration errors on feed intake of sows during lactation had the highest impact on lactation efficiency. A difference of 3 kg (10% of the standard deviation) changes the lactation efficiency by 1.5%.

Data collection

The lactation efficiency model was applied to individual sows at two farms: the experimental farm of the Institute for Pig Genetics (IPG), located in Beilen, the Netherlands, and the experimental farm of the Animal Sciences Group (ASG), located in Sterksel, the Netherlands. These farms used partly the same genetics, but were independent in terms of management. The association between lactation efficiency and other reproductive traits was studied within farm and compared between both farms. Components of the lactation efficiency model were calculated and compared to literature values.

Dataset IPG

Animals: Between October 2001 and December 2005, data on 363 commercial crossbred sows: TOPIGS20 (Dutch Large White×Dutch Landrace), TOPIGS30 (Daltrain×Dutch Landrace) and TOPIGS40 (Daltrain×Dutch LargeWhite), were available. The 'Daltrain' is a Piëtrain derived line, selected on maternal traits for over 30 years.

Traits: As standard farm protocol, each sow was weighed and ultrasonic backfat thickness was recorded on day of transfer to the farrowing house and again when the piglets were weaned. On average, sows entered the farrowing house 8.8 (range 5–22) d before the expected date of parturition. Live and stillborn piglets were recorded individually, including their weights at birth and at weaning, and their cross fostering and mortality data. Feed intake was recorded as the cumulative amount of feed per lactation.

Other traits of interest are: farrowing survival (number of piglets born alive as a percentage of live and stillborn piglets together), growth of piglets and mothering ability (number of piglets weaned as a percentage of number of piglets potentially to be weaned per sow (live born + balance of cross fostered piglets)). Traits of the subsequent cycle, included in the analyses, are: interval weaning–1st insemination and interval 1st insemination–pregnancy.

Feed: Net energy content of the commercial lactation diet, used at the IPG-farm, was 9.68 MJ NE/kg. Metabolisable energy was assumed at 13.5 MJ ME/kg. The feed supplied contained 147.2 g of crude protein and 8.1 g of lysine per kg diet. During lactation, sows were fed restrictedly. Primiparous sows were fed maximum 7 kg/d, and multiparous sows maximum 8 kg/d. From day of parturition, sows were fed according to an ascending scale until they reached the maximum at day 14 of lactation.

Weight of piglets at cross fostering was not available. If the farm manager decided a sow had to nurse a second litter within the same lactation, they received older piglets. The output of such a sow could not be established, because the starting point could not be set. Sows that had to nurse a second litter within the same lactation were excluded from the analyses.

Dataset ASG
Animals: Between October 2000 and February 2004, an experiment to study the effects of feeding group-housed gestating sows a low protein and low phosphorus diet, was performed (van der Peet-Schwering et al., 2005). A total of 185 crossbred gilts (Dutch Large White×Dutch Landrace) were allotted to a control or phase feeding treatment. The sows in the control group were fed a conventional diet during gestation. The sows in the phase feeding treatment group were fed a low protein, low phosphorus diet, during different periods from the beginning of gestation and then switched over to the conventional diet. Phase feeding during gestation increases the percentage of sows that returns to oestrus in parity 1 and 2

sows but not in older sows. Other reproductive traits were not affected by phase feeding. Therefore, experimental treatment was ignored in this dataset.

Traits: Body weight and ultrasonic backfat thickness were measured on each sow on day of transfer to the farrowing house, on average at day 108 of gestation, and again when the piglets were weaned during four parities. Number of total piglets born (live born piglets + stillborn piglets +mummies) was recorded within 16 h after parturition. Each live piglet was weighed at parturition, after cross fostering, and at weaning. In total 408 lactations of 150 sows (maximum 4 parities per sow) were available.

Feed: During gestation, the conventional diet contained 13.5% crude protein and 4.7 g/kg phosphorus. The experimental diet contained 11.8% crude protein and 4.1 g/kg phosphorus. During lactation, sows were fed according to an ascending scale from parturition until day six after parturition, and were given free access to the lactation diets from day six after parturition onwards. During lactation, a commercial lactation diet was fed to all sows. Piglets were given free access to a commercial creep feed from day 11 after birth until weaning.

Statistical analyses
To demonstrate the characteristics of the trait "lactation efficiency", two statistical techniques were used: correlations between lactation efficiency and reproduction traits and 50/50 high–low sampling within farm. Towards a better understanding of the trait lactation efficiency, the relation between input and output, for primiparous and multiparous sows, was described for both farms as well.

Lactation efficiency characteristics
To account for imbalanced distribution of observations over various fixed effects, data on reproduction traits were pre-adjusted for fixed effects (models (a)-(d)). To calculate correlations between lactation efficiency and reproduction traits, the observed lactation efficiency and residuals for reproduction traits were used. For maximum accuracy of residuals, different statistical models were used for different traits. Model (a) was used for most traits:

$Y_{ijkl} = \mu + PARITY_i + BATCH_j + LINE\ ♀_k + e_{ijkl}$ (a)

For feed intake, piglet growth and litter mass at weaning model (a) were extended with the co variable lactation length (model (b)).

$$Y_{ijkl} = \mu + PARITY_i + BATCH_j + LINE\,♀_k + b_1 \times LLE + e_{ijkl} \qquad\qquad \text{(b)}$$

For the trait mothering ability, the co variable: number of piglets to be weaned was added to model (b).

$$Y_{ijkl} = \mu + PARITY_i + BATCH_j + LINE\,♀_k + b_1 \times LLE + b_2 \times TBW + e_{ijkl} \qquad \text{(c)}$$

Finally for the traits, interval weaning to oestrus and interval first insemination to pregnancy, model (a) was extended with the number of piglets weaned in the preceding cycle (as a co variable), as well as the linear and quadratic term of lactation length.

$$Y_{ijkl} = \mu + PARITY_i + BATCH_j + LINE\,♀_k + b_1 \times NWND + b_2 \times LLE + b_3 \times LLE^2 + e_{ijkl} \qquad \text{(d)}$$

where: Y_{ijkl} = trait for sow l of parity i within batch j of line k; μ = population mean; PARITY = the parity of the sow. Parity 6 and higher were combined; BATCH = 3 weeks farrowing batch; LINE ♀ = the line code of the (crossbred) sow; LLE=lactation length (d); TBW=to be weaned (#); NWND= number of weaned piglets in the preceding cycle (#); and e_{ijkl} = error for sow l of parity i within batch j of line k.

To compare sows with high and low lactation efficiency, Least Squares Means were calculated for reproduction traits, using a classification. In models (a)-(d), where the classification was:

High/Low based on observed lactation efficiency.

Relation between output and input: The relation between output and input was described by a negative exponential growth curve, because it was likely that output would reach a plateau at a certain level of input. In situations where no plateau is encountered, this type of curve can describe a linear relation. A negative exponential growth curve was fitted using the Non Linear procedure (PROC NLIN) in SAS/STAT software (SAS, 1989), using the Marquardt-method as an iterative solver.

2.3 Results

Reproduction

Reproduction results for two farms, IPG and ASG are displayed in Table 2.2. Levels of performance during lactation might affect interval weaning–oestrus or interval insemination–pregnancy in the next cycle. These intervals are also shown in Table 2.2. The lower number of observations on interval weaning–oestrus compared to the number of cycles is caused by culling of sows in IPG, while culling and

Table 2.2 Reproduction results on two farm: IPG and ASG.

	IPG[1]				ASG[2]			
	n	*Mean*	*Min.*	*Max.*	*n*	*Mean*	*Min.*	*Max.*
Parity	913	3.2	1	8	409	2.2	1	4
Total Number Born, n		12.7	2	21		12.4	3	25
Number Born alive, n		11.7	2	20		11.9	3	21
Farrowing survival, %		93.5	35.3	100		96.2	66.7	100
Mothering ability, %		86.3	30.0	100		92.7	46.7	100
Weaned, n		9.9	5	14		10.6	6	14
Lactation period, d		25.9	15	45		26.3	18	38
Interval weaning-oestrus, d	810	6.8	0	47	272	6.4	3	44
Interval insemination-pregnancy, d	770	2.6	0	131		2.7	0	65

[1] Experimental farm of Institute for Pig Genetics (IPG), Beilen, the Netherlands;
[2] Experimental farm of Animal Sciences Group (ASG), Sterksel, the Netherlands.

availability of data caused the lower number in ASG. The experiment at ASG stopped when sows weaned their fourth litter. Intervals were therefore only available for parities 2 and 3. Only for sows that produced a subsequent litter, was the insemination–pregnancy interval known.

The reproduction results of IPG originated from an operating farm, while, reproduction result of ASG came from an experiment with an end date. Average parity differed, and therefore, total number born as well. The most striking difference between the two farms was the difference in survival of piglets. Farrowing survival was higher on ASG which resulted in a higher number born alive compared to IPG, although total number born was lower. Survival of live born piglets until weaning (mothering ability) was also higher on ASG. Higher farrowing survival and mothering ability on ASG compared to IPG averaged 0.7 more piglets weaned per litter. Differences in lactation period and intervals were small, comparing both farms.

Descriptive statistics of the LE model

Table 2.3 shows the mean, minimum and maximum of traits affecting input and/or output and thus lactation efficiency on two farms: IPG and ASG. On average, lactation efficiency was 68% on IPG and 65% on ASG. The minimum lactation efficiency was 27%; the maximum exceeded 100% (124%). Biologically, an energy efficiency of over 100% cannot exist. Although outliers in underlying traits (larger than average +4 times standard deviation; or smaller than average minus 4 times standard deviation) were removed from the dataset, recording errors and

Table 2.3 Mean, minimum and maximum of the lactation efficiency model traits, on two farms: IPG and ASG.

		IPG[1]			ASG[2]		
		Mean	*Min.*	*Max.*	*Mean*	*Min.*	*Max.*
Input	Weight at transfer to the farrowing house, kg	241	150	353	229	164	307
	Start weight, kg	218	129	331	206	152	277
	Weight of live + stillborn piglets at birth, kg	17.9	3.4	30.9	18.4	5.4	30.9
	Backfat at transfer to the farrowing house, mm	17.6	7.5	38.0	17.3	9.0	27.3
	Estimated protein mass at start of lactation, kg	33.8	20.5	53.2	31.7	21.9	43.7
	Estimated fat mass at start of lactation, kg	44.3	22.6	90.9	42.5	25.1	66.7
	Weaning weight, kg	207	118	339	188	115	266
	End weight, kg	205	116	339	186	113	264
	Backfat at end of lactation, mm	14.4	6.5	29.0	13.1	6.0	22.3
	Estimated protein mass at end of lactation, kg	32.5	19.3	54.6	29.6	17.1	42.2
	Estimated fat mass at end of lactation, kg	36.9	13.9	70.9	32.5	15.4	55.3
	Weight losses sow, kg	13.1	-33.9	65.7	19.9	-24.6	61.2
	Protein losses sow, kg	1.2	-6.1	10.1	2.1	-5.4	9.6
	Fat losses sow, kg	7.5	-9.7	38.1	10.0	-6.7	25.3
	Total feed intake during lactation, kg	139.9	36.3	307.0	135.3	62.7	188.9
	Energy from feed and body reserves, MJ ME/d	85.0	40.5	120.1	86.3	49.6	114.2
	Maintenance Sow, MJ ME/d	24.4	16.2	34.5	23.0	17.4	29.3
	Input, MJ ME/d	60.6	18.5	96.3	63.3	27.4	90.8
Output	Weight of living piglets after cross fostering, kg	16.8	9.0	30.9	17.0	7.8	25.4
	Protein mass at birth of live born piglets, kg	1.95	1.04	3.59	1.98	0.90	2.95
	Fat mass at birth of the live born piglets, kg	0.23	0.13	0.43	0.24	0.11	0.36
	Litter weight at weaning, kg	78.5	25.7	154.5	81.2	36.0	112.8
	Protein mass at weaning, kg	11.9	3.8	24.0	12.4	5.9	17.3
	Fat mass at weaning, kg	11.2	2.9	24.7	11.2	4.5	16.3
	Weight of the dead piglets, kg	2.9	0	23.6	1.0	0	9.3
	Maintenance piglets, MJ ME/d	14.0	6.1	22.3	14.6	6.9	19.4
	Output, MJ ME/d	40.4	13.9	60.0	40.5	17.3	54.3
	Lactation efficiency, %	68	34	124	65	27	108

[1] Experimental farm of Institute for Pig Genetics (IPG), Beilen, the Netherlands;
[2] Experimental farm of Animal Sciences Group (ASG), Sterksel, the Netherlands.

imperfection of the lactation efficiency model probably caused this. On IPG only 14 of 913 (1.5%) and on ASG only 3 of 409 (0.7%) showed an efficiency of over 100%.

On IPG, sows lost on average about 13 (218–205) kg of weight during lactation. Fat and lean (four times the protein mass) represented 94% of the total body weight change during lactation. Gut fill and ash contributed to the remainder. Proportionally, about 57% of the weight loss in sows was fat and 37% was lean. Sows on ASG lost more weight during lactation, about 20 (206–186) kg of which 50% was fat and 42% lean. There were large differences between sows in their weight loss: some sows lost up to 66 kg (fivefold the average), whereas others gained almost 34 kg. Large differences were also found for litter weight at weaning. One sow produced 154.5 kg of piglets at weaning, another only 25.7 kg.

The energy output in piglets on both farms was similar (40.4 and 40.5 MJ ME/d); although on IPG energy deposition shifted towards piglets which did not survive the lactation (the mortality until weaning amongst live born piglets was higher on IPG, compared to ASG). On ASG, sows were fed ad lib; on IPG sows were fed restricted. Despite this, feed intake was higher on IPG than on ASG. Weight losses, on the other hand, were higher on ASG than on IPG.

The difference between the observed weight of the sow at the end of the lactation and the calculated end weight represented the estimated water weight gain of the mammary gland. On average, this difference was 1.7 kg on both farms. The difference between the two extreme values was 5.1 kg on IPG and 3.8 kg on ASG (results not shown). The 5.1 kg on IPG represented 5.3 MJ ME/d of a 25-day lactation period, assuming the weight loss was 60% fat and 35% lean. 5.3 MJ ME/d is almost 10% of the average input. On average, water weight gain of the mammary gland was of minor importance. However, by ignoring this, lactation efficiency of highly productive sows will be overestimated.
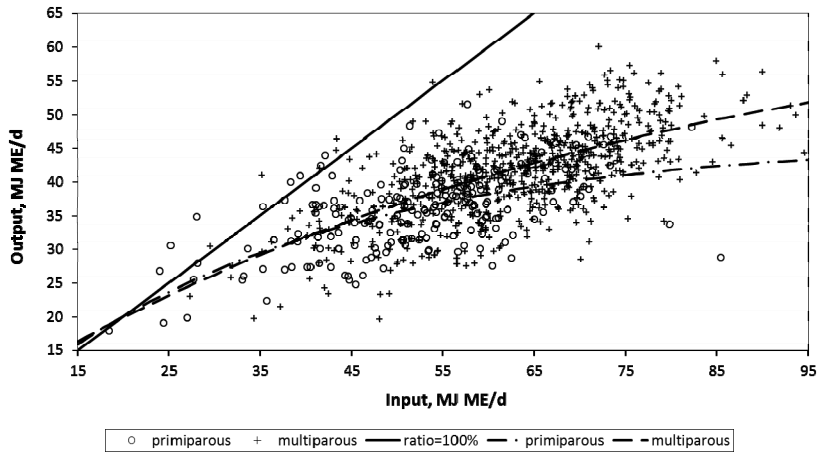
The relation between output and input
The relation between input and output on IPG is in Figure 2.2 and on ASG in Figure 2.3. The straight line is the line where 1 MJ ME/d led to 1 MJ ME/d output, indicating a lactation efficiency of 100%.

On IPG, regression equation of output on input for primiparous sows was

$$Output_{primiparous} = 47.2344 \times [1 - e^{(-0.0299 \times Input)}] - 1.2 \qquad (R^2 = 0.37)$$

and for multiparous sows was

$$Output_{multiparous} = 65.3033 \times [1 - e^{(-0.0138 \times Input)}] + 4.1 \qquad (R^2 = 0.40)$$

Figure 2.2 The relation between output and input on IPG.

The relation between output and input is of diminishing returns-type (the principle that towards higher input, progress runs out). For both primiparous and multiparous sows, the plateau of the estimated regression was not reached within the observed variation of input. For primiparous sows the plateau will be reached at a lower input level.

The relation between output and input on ASG was less clear, both for primiparous and multiparous sows. For primiparous sows, the relation was still of diminishing returns-type, but R^2 was low. Fitting a negative exponential growth curve instead of a linear regression for multiparous sows did not improve R^2 (results not shown). On ASG, regression equation of output on input for primiparous sows was

$$Output_{primiparous} = 36.596 \times \left[1 - e^{(-0.0326 \times Input)}\right] + 6.5 \qquad (R^2=0.16)$$

and for multiparous sows was

$$Output_{multiparous} = 486.7 \times \left[1 - e^{(-0.00077 \times Input)}\right] + 18.2 \qquad (R^2=0.38)$$

The maximum observed output on ASG was lower than on IPG (54.3 MJ ME/d on ASG and 60 MJ ME/d on IPG). This might explain why the relation between output and input on ASG was not clearly of diminishing returns type. The maximum output for primiparous sows was lower than for multiparous sows on both farms.
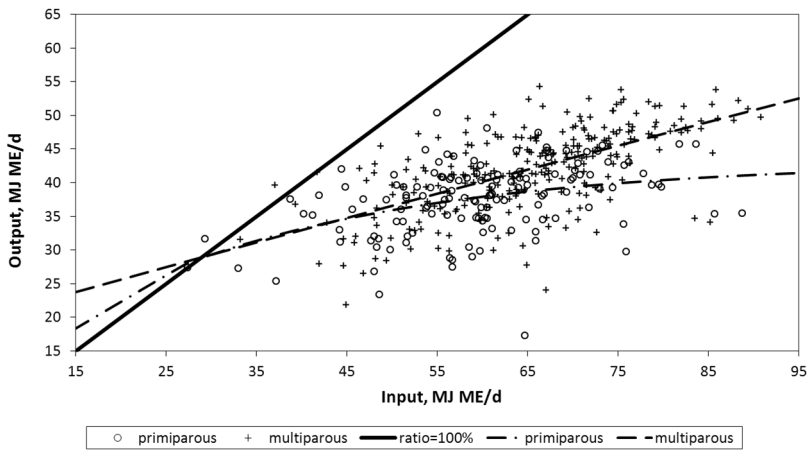
Figure 2.3 The relation between output and input on ASG.

Relation between lactation efficiency and reproduction traits

Correlations between residuals from the models (a)–(d) and lactation efficiency are in Table 2.4. There was a negative correlation between lactation efficiency and input (−0.48 on IPG and −0.57 on ASG). Two components of the input, i.e. fat losses of the sow and feed intake, were responsible for this correlation. Protein losses were uncorrelated with efficiency. Efficient sows showed a high output, although the correlation between efficiency and output was not as strong as the correlation of efficiency and input. Efficient sows showed a higher mothering ability (higher survival amongst their piglets) and a higher piglet growth till weaning, accumulated in a higher litter weight at weaning (correlations of 0.23 on IPG and 0.28 on ASG). Efficiency was not correlated with the intervals following the present lactation. Results were remarkably similar for the two farms.

High/low sampling

To demonstrate the characteristics of lactation efficiency, observations were split within farms. One group contained the 50% cycles with the highest calculated lactation efficiency; the other group contained the 50% with the lowest value. In Table 2.5 the Least Squares Means of the highest 50%-group are given along with the difference between the high and low groups. Significances of the relationship between lactation efficiency and reproduction traits are given for the correlations in Table 2.4.

Table 2.4 Correlation coefficients between lactation efficiency and residuals of reproduction traits, applying model (a) to (d), on two farms: IPG and ASG.

Reproduction trait	IPG[1]		ASG[2]	
	r	p-value[3]	r	p-value[3]
Number of lactations	913		409	
Start weight, kg	0.03	n.s.	0.08	n.s.
Protein mass at start, kg	0.11	0.001	0.13	0.008
Fat mass at start, kg	-0.13	0.001	-0.08	n.s.
End weight, kg	0.07	0.029	0.13	0.009
Weight loss, kg	-0.06	n.s.	-0.09	n.s.
Protein loss, kg	0.06	n.s.	0.01	n.s.
Fat loss, kg	-0.35	0.001	-0.29	0.001
Gestation length, d	0.09	0.006	0.01	n.s.
Live born, n	-0.04	n.s.	-0.05	n.s.
Average weight at birth, g	0.01	n.s.	0.06	n.s.
Standard deviation birth weight, g [4]	-0.04	n.s.		
Farrowing survival, %	0.05	n.s.	0.02	n.s.
To be weaned, n	0.11	0.001	0.04	n.s.
Average birth weight after cross fostering, kg	0.06	n.s.	0.07	n.s.
Std. dev. birth weight after cross fostering, g [4]	0.01	n.s.		
Feed intake during lactation, kg	-0.27	0.001	-0.35	0.001
Weaned, n	0.16	0.001	0.15	0.002
Mothering ability, %	0.12	0.001	0.16	0.001
Growth of the piglets till weaning, g/d	0.16	0.001	0.23	0.001
Litter weight at weaning, kg	0.23	0.001	0.28	0.001
Standard deviation weaning weight, g [4]	-0.08	0.014		
Interval weaning – 1st insemination, d	-0.02	n.s.	-0.08	n.s.
Interval 1st insemination – pregnancy, d	-0.01	n.s.	-0.09	n.s.
Maintenance sow, MJ ME/d	0.06	n.s.	0.11	0.022
Input, MJ ME/d	-0.48	0.001	-0.57	0.001
Output, MJ ME/d	0.23	0.001	0.30	0.001

[1] Experimental farm of Institute for Pig Genetics (IPG), Beilen, the Netherlands;
[2] Experimental farm of Animal Sciences Group (ASG), Sterksel, the Netherlands;
[3] n.s.= Not significant (p >0.05);
[4] Weight of the individual piglets was not available for ASG.

The difference in efficiency between the high and low groups was 17% on IPG and 15% on ASG. Efficient sows were slightly leaner at start of lactation and lost less fat during lactation, while their feed intake was less, compared to inefficient sows. As a

Table 2.5 Differences between high- and low efficiency sow, on two farms: IPG and ASG (Least Squares Means, applying model (a) to (d)).

	IPG[1]		ASG[2]	
	Highest 50%	*Difference High - Low*	*Highest 50%*	*Difference High - Low*
Number of lactations	457		205	
Lactation efficiency, %	76	+17	73	+15
Start weight, kg	230	+2	206	+3
Protein mass at start, kg	35.8	+0.6	31.8	+0.8
Fat mass at start, kg	45.3	-1.5	42.7	-1.4
End weight, kg	218	+2	187	+4
Weight loss, kg	11.5	0.0	19.8	0.0
Protein loss, kg	1.2	+0.4	2.3	+0.4
Fat loss, kg	6.2	-2.7	8.8	-2.3
Gestation length, d	115.8	+0.4	115.0	-0.1
Live born, n	11.54	-0.42	12.10	-0.43
Average weight at birth, g	1.47	+0.02	1.57	+0.03
Standard deviation birth weight, g	270	-7	-	-
Farrowing survival, %	92.6	+0.5	95.9	+0.7
To be weaned, n	11.74	+0.14	11.50	0.00
Average birth weight after cross fostering, kg	1.45	+0.06	1.57	+0.03
Std. dev. birth weight after cross fostering, g	231	-1	-	-
Feed intake lactation, kg	136.7	-8.4	132.2	-10.6
Weaned, n	9.99	+0.33	10.91	+0.21
Mothering ability, %	87.1	+2.1	95.2	+1.9
Growth till weaning, g/d	258	+13	242	+12
Litter weight at weaning, kg	81.1	+6.3	85.9	+5.1
Standard deviation weaning weight, g	1364	-67	-	-
Interval weaning – 1st insemination, d	6.2	-0.2	5.1	-1.0
Interval 1st insemination – pregnancy, d	3.2	+1.5	2.3	+0.2
Maintenance sow, MJ ME/d	25.4	+0.2	23.0	+0.3
Input, MJ ME/d	55.8	-8.7	60.0	-9.3
Output, MJ ME/d	41.9	+3.0	42.7	+2.7

[1] Experimental farm of Institute for Pig Genetics (IPG), Beilen, the Netherlands;
[2] Experimental farm of Animal Sciences Group (ASG), Sterksel, the Netherlands.

result, their total energy input was over 15% lower on both farms. Despite the lower input, efficient sows produced over 6% more (energy) output in piglets.

Litter size, birth weight, standard deviation of birth weight at birth and farrowing survival were not different between groups (Table 2.4). Efficient sows had to take

care of a slightly higher number of piglets at the IPG-farm. Average birth weight after cross fostering and the variation within a litter (after cross fostering) showed no relation with the efficiency of the foster sow.

Despite differences in levels of traits between the IPG-farm and the ASG-farm, differences between high and low sows were remarkably similar at both farms. Weight losses during lactation at the ASG-farm were almost doubled compared to the IPG-farm, despite ad lib feeding of sows at the ASG-farm. Output was similar at both farms, but input was much lower at the IPG-farm because of lower mobilization from body stores, resulting in higher lactation efficiency. Efficient sows were the better mothers, because their mothering ability was higher, resulting in a higher number of weaned piglets, and daily gain of the piglets was higher too. This was valid for the IPG-farm, where mortality until weaning amongst live born piglets was relatively high, but also for the ASG-farm, where mortality was relatively low.

Piglet weight variation within a litter is a source of concern in modern swine management systems because a high variation delays pig movement through consecutive phases of production. The standard deviation of weight at weaning in the high lactation efficiency group was 67 g lower than in the low lactation efficiency group. So the weaned piglets were more uniform when fostered by an efficient sow.

2.4 Discussion

Feed efficiency by means of feed conversion ratio or residual feed intake is a known and important characteristic in finishing pigs. The present investigation is the first attempt to define feed efficiency in lactating sows. Results of our study indicate that differences in lactation efficiency between sows exist. At specialized finisher producing farms, around 33% of the cost price of a piglet of 25 kg are costs of feed (Den Ouden et al., 1997). Increasing lactation feed efficiency is also economically relevant, an increase of 10% would reduce the amount of feed needed per sow and year by 40 kg for the hypothetical sow from Table 2.1. Besides being economically important in itself, this might help to prevent negative effects of increased litter size at birth, for example an increased interval weaning to oestrus. Efficient sows showed reduced litter mortality. Mortality itself is economically relevant. Reduced litter mortality will be beneficial for public acceptance too since societal concerns about animal welfare in intensive production systems are increasing (Swanson, 1995).

Applying the lactation efficiency model for two farms yielded remarkably similar results, despite different feeding strategies (restricted versus ad lib). To test whether the different components of the lactation efficiency model were estimated accurately, three different validations were performed.

Validation of the lactation efficiency model

Validation 1: energy metabolism compared to balance trials

Table 2.6 compares our estimates of components of energy balance in lactating and of 1 kg sows over three lactations to those of Everts and Dekker (1994b). Most of the formulas used were derived from their experiments. Parts of these experiments were balance trials. The number of lactations per lactation diet was not equally distributed. Therefore in Table 2.6 the weighted averages according to the number of observations per diet are given for Everts and Dekker (1994b).

The balance trials were performed from day 4 to day 25 of lactation. Mortality was not reported, but since trials started at day 4, it is likely that the reported litter size was the number of piglets weaned. Therefore, also for IPG as well as for ASG, reported litter size is the number of piglets weaned. Everts and Dekker (1994b) calculated litter energy gain from the body composition of piglets at weaning. From this, formulas were derived to estimate body composition depending on piglet gain. The differences in litter energy gain between our results and those of Everts and Dekker (1994b) were the direct result of differences in piglet gain.

The ME intake of sows in the experiment of Everts and Dekker (1994b) was somewhat underestimated, because energy losses in faeces and urine of the suckling piglets were included in those of the sows. According to Everts and Dekker (1994b), the ME intake should be multiplied with about 1.07 to obtain the actual ME intake of sows. In Table 2.6 this multiplication is already done.

The ratio between 'litter energy gain' and 'energy from feed and body mobilization' was remarkably similar, both between experiments and between parities. At different levels of feed intake and mobilization from body stores, approximately 30% of the energy was deposited in litter energy gain. 'Energy from feed and body mobilization' was higher in the experiments of Everts and Dekker (1994b), mainly because energy mobilization (per day) from body stores was higher, with a higher litter energy gain and thus higher piglet growth as a result.

The experiments of Everts and Dekker were executed from July 1986 until February 1990, a difference of over 15 years compared to the data collection on IPG and ASG. It is unlikely that the genetic potential for piglet growth became limiting during these years. If piglets are artificially reared from birth, they are capable of

Table 2.6 Mean components of the energy balance (uncorrected averages) in sow over lactation, on two farms: IPG and ASG, compared to the balance trials of Everts and Dekker (1994b).

		Everts and Dekker[1]			IPG[2]			ASG[3]		
Sows	Parity	1	2	3	1	2	3	1	2	3
	Number of sows	23	17	16	214	183	152	141	110	88
	Mean live weight sow, kg	174	195	208	169	199	216	173	198	211
	Weight losses sow, kg	15.0	13.9	18.4	12.0	15.3	15.2	19.8	20.0	21.6
	Protein losses sow, kg[4][5]	1.2	1.5	1.9	1.1	1.5	1.6	2.0	2.1	2.4
	Fat losses sow, kg[5]	9.0	10.5	10.5	6.9	8.2	7.9	10.3	10.0	10.3
	ME intake, MJ/d[6]	66.8	73.7	73.8	61.4	74.0	75.7	63.3	69.7	74.4
	Body mobilization, MJ ME/d	18.2	21.4	21.9	11.7	13.8	13.4	17.2	17.2	17.7
	ME intake+body mob., MJ ME/d[6]	85.0	95.1	95.7	73.0	87.9	89.0	80.6	86.9	92.1
Piglets	Piglets weaned, n	9.9	10.5	10.6	9.5	10.1	10.0	10.4	10.4	10.7
	Piglet growth till weaning, g/d	254	266	273	231	258	255	221	241	246
	Litter weight gain, kg/d	2.46	2.79	2.88	2.19	2.60	2.58	2.28	2.49	2.61
	Litter energy gain, MJ ME/d	25.4	29.3	29.4	22.9	27.6	27.4	23.7	26.1	27.4
Efficiency	Ratio (LEG / ME + b.mob.)[7]	30	31	31	32	32	31	30	30	30
	Lactation efficiency, %	-	-	-	70	66	66	65	64	63

[1] Adapted from Everts and Dekker (1994b);
[2] Experimental farm of Institute for Pig Genetics (IPG), Beilen, the Netherlands;
[3] Experimental farm of Animal Sciences Group (ASG), Sterksel, the Netherlands;
[4] Tissue protein = N×6.25;
[5] The energy content of 1 kg fat is assumed to be 39.5 MJ ME protein 23.8 MJ ME;
[6] ME intake×1.07 (see text);
[7] (Litter energy gain, MJ ME/d×100) / (ME intake + body mobilization, MJ ME/d).

growing at least at twice the rate than if they are suckled by the sow during lactation (Hodge, 1974).

Through selection, sows might have been changed during this period. Whittemore and Morgan (1990) concluded that lactating sows appeared unwilling to mobilize fat stores when (P2) backfat falls below 10 mm and when the lipid:protein ratio in the whole body falls below 1:1. This would suggest that lean genotypes of sows may be less likely to mobilize from body stores for milk production than fatter genotypes.

The fat content of the body mobilization is 60%, 76% and 57% for 1st, 2nd and 3rd parities respectively in the experiments of Everts and Dekker. This is higher than on IPG (57%, 54% and 52%) and on ASG (52%, 50% and 48%). 2nd parity sows lost on average 13.9 kg of weight during 21 d in the experiments of Everts and Dekker.

However, 10.5 kg fat loss and 6.0 kg lean loss together exceeded that weight loss by 2.6 kg.

The lactation efficiency model applied on IPG and on ASG yielded similar results as to those found in respiration chambers by Everts and Dekker (1994b). The ratio between litter energy gain and energy from feed and body mobilization was remarkably similar between both parities and experiments.

Mobilization from body stores was higher in the experiments of Everts and Dekker. This can be explained by the number of years between the experiments of Everts and Dekker and our data collection. Sows might have been changed genetically over the years.

Validation 2: dynamics of body composition of sows

On IPG, sows lost on average about 13 kg of weight. Proportionally about 57% of the weight loss was fat and 37% lean. Sows on ASG lost more weight during lactation, almost 20 kg of which 50% was fat and 42% lean. The amount of fat as a proportion of body weight loss varies from 50% to 69% according to Mullan (1991) in a review article. Fat losses on IPG and ASG were within this range.

Mullan et al. (1993), using a factorial method, predicted that a sow weighing 160 kg post-partum, consuming 68 MJ ME and 840 g crude protein per day and suckling 10 piglets each gaining 200 g/d, would loose 13.8 kg body weight during a 4-week lactation. Of this, proportionally 64% would comprise fat and 32% lean. Based upon the relations estimated in data from IPG, a sow consuming 68 MJ ME/d and suckling 10 piglets each gaining 200 g/d would lose 12.0 kg during a 4-week lactation, of which 7.1 kg (59%) was fat and 1.1 kg protein (37% lean). These results are in line with the finding of Mullan et al. (1993). The predicted weight loss was slightly lower than in the example of Mullan. The fat content of the weight loss was 5% lower and the lean content 5% higher. Given the feed composition on IPG, sows consuming 68 MJ ME/d would have consumed 740 g crude protein per day, a 12% reduction compared to the example of Mullan.

The dynamics of body composition of sows as calculated with the lactation efficiency model were in line with results from literature.

Validation 3: milk energy balance

The milk energy balance, defined as the difference between the milk energy output and the energy required for litter gain and maintenance of the piglets, should be zero. On both farms, more energy was deposited in piglets than was produced by the sow through energy in milk. This suggests that energy gain in piglets was overestimated. On IPG, the milk energy balance was −5.8 MJ/d of lactation, or less

than 10% of the daily input. On ASG, there was a calculated shortage of less than 5% of the daily input (−3.1 MJ/d). Apart from registration errors and imperfection of the lactation efficiency model, other possible explanations were:

- Piglets were given free access to a commercial creep feed on both farms. Feed intake by piglets, however, was not recorded. The intake was estimated at 200–300 g per piglet during a 26-day lactation. An intake of 250 g of feed per piglet by a litter of 10 piglets corresponds to 1.3 MJ/d of lactation per sow, which was not taken into account in the model;
- Weight of the piglets that died during the suckling period was assumed to be the average of the weaned piglets at the age of mortality. This is probably an overestimate which contributes to overestimation of the output. This is especially true for IPG, where mortality was high;
- Activity of ad libitum fed sows is higher compared to restrictedly fed sows, because their feed intake frequency is higher. This might explain why Noblet and Etienne (1987) found that heat production of energy restricted sows was significantly lower. A lower heat production as a consequence of lower activity means less energy needed for maintenance and more energy available for the production of milk. As a consequence of different feeding strategies there might be some differences in maintenance of sows between IPG and ASG, which were not taken into account;
- Mobilization of fat and protein of sows and deposition of fat and protein of sows were assumed to be energetically equal to each other (with a different sign). In 28% of the lactations on IPG (n=254), fat mass or protein mass of sows increased. In 40 lactations, both fat mass and protein mass increased (4%). If the assumption that mobilization and deposition are energetically equal is not true, it affects a high number of lactations;
- Through genetic selection towards leaner slaughter pigs, it is likely that fat percentage of growth during early life of modern piglets had reduced since the experiments of Everts and Dekker (1994a, b). This would explain why litter energy gain was overestimated. Table 2.1 indicates that after feed energy contents, 10% deviation in fat deposition of piglets is the second most severe source of variation in lactation efficiency.

To address the last 5 to 10% energy, a more extensive recording structure (feed intake piglets, weight of died piglets) and some adaptations of the lactation efficiency model to modern pigs are necessary. However, current approach already helps towards a better understanding.

Lactation efficiency, the trait

There were differences in energy efficiency during lactation amongst sows. The most efficient sows are the most promising. Remarkable differences between the 50% most efficient sows and the other 50% were:

• Efficient sows were efficient mainly because their feed intake and fat losses were reduced, at an output level which was slightly higher;
• The more efficient sows were the better mothers. Mortality of their piglets was lower and growth rate of the piglets was higher. At weaning their litters were more uniform.

Efficient sows may not waste energy in activity. Therefore, there was more energy available for the production of milk (maintenance is overestimated). The low activity of sows is likely to be favourable for pre-weaning survival of piglets.

On ASG, feed intake was ad libitum from day 6 onwards. Efficient sows showed a lower feed intake and a higher protein mass at start of lactation. A similar phenomenon was seen in finishing pigs, where genetically lean and efficient pigs showed a lower appetite (Kanis, 1990). Another explanation of why efficient sows showed a lower feed intake could be a higher frequency of 'overeating' or temporary food refusals in the group of efficient sows. Overeating would result in a major drop in feed intake during lactation. The maximum amount of feed a sow can consume per day was not affected (feed intake capacity) but as a result the total feed intake during lactation decreased. This could be the situation where the most efficient sows were more susceptible to environmental changes, for example sudden room temperature rises (heat stress).

Feeding on IPG during lactation was restricted. Feeding on ASG was ad libitum from day 6 onwards. The correlations found were very similar. Apparently feeding strategy did not affect the relations between lactation efficiency and other reproductive traits.

Efficient sows showed less mobilization of fat during lactation. This was perhaps unexpected. Energy from body stores can be converted efficiently (assumed efficiency is 88%) to milk energy. Only 72% of the energy from feed was assumed to be converted into milk energy. Since these percentages were not part of the trait lactation efficiency, one would expect that efficient sows used more energy efficient sources than inefficient sows.

Application

Data collection on IPG as well as on ASG was performed with as few interventions as possible, for the sow and her piglets. For example: weight of sows was recorded at transfer to the farrowing house, on IPG on average 8.8 d before parturition. The weight of the sow shortly after parturition was the weight of interest. Weighing just after the actual farrowing was considered a real risk for the sow and her piglets. Weighing was therefore necessarily too early. Available formulas for the development of weight of foetuses and uterine fluid appear to be very useful in adjusting for the differences in days, especially since this is a posterior correction and number of actual foetuses is known.

All three validations showed that an accurate recording structure for lactation feed intake, body composition changes and relevant reproduction traits with little intervention is possible on commercial farms. Applying this recording structure for a limited period of time on any farm would give a lot of information on the lactation performance of sows and piglets of that farm, which is also economically relevant. The lactation efficiency model could therefore be used as a tool for farm management advisory. Errors in energy intake through feed had the highest impact on lactation efficiency. To take maximum advantage of such a tool, it should be possible to register feed intake and energy content of feed accurately. Based on observations on IPG and ASG, the suggestion was made that the maximum output a sow could produce was about 60 MJ/d. It would be interesting to see if there are farms that exceed the output of 60 MJ/d. On IPG and ASG as well as during the experiment of Everts and Dekker (1994b), primiparous sows had a lower litter energy gain than second and third parity sows. Further research is needed to investigate whether this phenomenon is biologically determined.

2.5 Conclusions

Lactation efficiency is defined as an energy efficiency of sows. The higher lactation efficiency the more of the available energy through feed intake and mobilization from body stores above maintenance of the sow (input) is used for piglet growth and maintenance (output). Estimates of various components of energy input and output fit well to literature values.

Extra input, by means of feed intake or mobilization from body stores will generate extra output by means of litter mass at weaning. There might be a maximum to the output a sow can produce. This maximum will be lower for primiparous sows.

Our results indicate that differences in energy efficiency between sows exist. Lactation efficiency was calculated for individual sows on two farms. Results were

remarkably similar for the two farms, even though feeding strategies were different. Efficient sows were efficient, mainly because their feed intake and fat losses were lower, while their output was slightly higher. The more efficient sows were the better mothers. Mortality of their piglets was lower and growth rate of their piglets was higher. At weaning their litters were more uniform. Results suggest different behaviour between efficient and less efficient sows, however, this question should be addressed.

Application of the model presented in this study facilitates future research on genetics of lactation efficiency and related maternal traits.

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Appendix

Formulas used to estimate the energy content of various sources of energy were derived from experiments of Everts and Dekker (1994a), unless stated otherwise.

Input definitions
Changes in body composition between start and end of lactation are usually not available as such. These changes have to be estimated therefore, based on weight and backfat recording of sows and weight recording of piglets.
Protein and fat content of sows were estimated as:

$$Protein, kg = +1.90 + 0.1711 \; x \; Body\;weight, kg - 0.3113 \; x \; Backfat, mm \qquad (4)$$

$$Fat, kg = -11.58 + 0.1027 \; x \; Body\;weight, kg + 1.904 \; x \; Backfat, mm \qquad (5)$$

The energy content of 1 kg protein was set at 23.8 MJ ME and 1 kg fat at 39.5 MJ ME (Everts et al., 1995).

Start weight of sows
The weight of the sow just after parturition is the weight of interest. If body weight (and backfat) of a sow were recorded only before parturition, then weight of sows was adjusted for weight of foetuses, weight of placenta and weight of intra-uterine fluid, as described by Noblet et al. (1985):

$$Total\;weight\;foetuses, g = e^{(8.72962-4.07466 \times e^{(-0.03318 \times (d-45))}+0.000154 \times f \times d + 0.06774 \times n)} \qquad (6)$$

$$Weight\;placenta's, g = e^{(7.02746-0.95164 \times e^{(-0.06879 \times (d-45))}+0.000085 \times f \times d + 0.09335 \times n)} \qquad (7)$$

$$Weight\;intra\text{-}uterine\;fluid, g = e^{(-0.2636+0.18805 \times d - 0.001189 \times d^2 + 013194 \times n)} \qquad (8)$$

where d = days of pregnancy; f = energy intake during gestation (MJ ME/d); and n = number of foetuses.
From equations (6)-(8), the ratio between total intra-uterine weight (foetus + placenta + intra-uterine fluid) and weight of foetus (live born + stillborn + mummified) was calculated to estimate weight loss of a sow after parturition:

$$Start\;weight, kg = Recorded\;weight, kg - litter\;weight\;at\;birth, kg \times \qquad (9)$$

$$\left[\frac{(Total\ foetus\ wt\ at\ d_w + \ placenta\ wt\ at\ d_w + \ intra\text{-}uterine\ fluid\ wt\ at\ d_w)}{Total\ foetus\ wt\ at\ d_p} \right]$$

where d_w = day of pregnancy when weight of the sow was recorded; d_p = day of pregnancy at parturition. Weight gain of the sow between transfer to the farrowing house and parturition was assumed to be negligible. Whether this assumption is true depends on parity, number of piglets born, and individual feeding scheme during gestation (Close and Cole, 2001).

End weight of sows

Weighing sows only at start and end of lactation underestimates loss of body weight because water content of mammary glands is assumed to be equal at start and end of lactation. If milk production increases, however, water content of mammary glands increases (Kim et al., 1999b). By ignoring this, body weight loss of high producing sows will be underestimated. A correction for water content of mammary glands was developed, based on experiments of Kim et al. (1999a,b, 2000). The estimated water gain of the mammary gland was subtracted from the observed weight of the sow at weaning.

$$End\ weight, kg\ = \ Recorded\ weaning\ weight\ - \tag{10}$$
$$\left\{ \left[(NFG - no.piglets\ weaned) \times 73 + (no.piglets\ weaned \times 146.15 + 2.17 \times ADG) \right.\right.$$
$$\left.\left. \times \left(1 - \frac{DM_{weaning}}{100} \right) - NFG \times 431.5 \times \left(1 - \frac{DM_{parturition}}{100} \right) \right] / 1000 \right\}$$

where NFG = number of functional glands at parturition (assumed to equal the number of piglets to be weaned + 1 with a maximum value of 15, in case the number of functional glands is omitted).

Kim et al. (1999a) measured the dry tissue content of the mammary gland from dissections on day 0, 5, 10, 14, 21 and 28 of lactation. They reported a significant ($p<0.05$) linear and quadratic effect of day of lactation (DL) on dry tissue percentage. Based on the given Least Squares Means per day of lactation the following formula was derived:

$$\%\ Dry\ tissue\ (DM)\ = \ 31.805\ -\ 0.6027\ x\ DL\ +0.011\ x\ DL^2\ (R^2 = 0.85) \tag{11}$$

There was no effect of litter size on percentage of dry tissue in individual nursed glands (Kim et al., 1999b).

Maintenance

The ME needed for maintenance of a sow was calculated as:

$$Maintenance, MJ\ ME/d\ =\ 0.440 \times (average\ weight, kg)^{0.75} \tag{12}$$

where average weight is the average of start weight and end weight of the sow.

Output definitions

Fat and protein mass of a piglet at weaning is the amount at birth plus the amount added between birth and weaning. For body composition of piglets at birth, the assumed percentages were 1.4 % fat and 11.6 % protein (tissue protein = N x 6.25), representing the calculated mean value from literature by Everts and Dekker (1994a). Lipid deposition depends on piglet growth rate (ADG in g/d).

$$Fat\ mass, kg = birth\ weight \times 0.014 + \tag{13}$$
$$(weaning\ weight - birth\ weight) \times (0.135 + 0.00014 \times ADG)$$

Protein deposition is assumed independent of growth rate.

$$Protein\ mass, kg = birth\ weight \times 0.116 + \tag{14}$$
$$(waening\ weight - birth\ weight) \times 0.16$$

If the weight of piglets that died was not recorded, but mortality date was known, then the weight at the day of mortality was estimated based upon growth of their littermates and age at mortality. Everts et al. (1995) gave the relative piglet growth in the different weeks of lactation. The daily gain for week of lactation 1, 2, 3 and 4 was 80, 105, 110 and 105%, respectively, of the average daily gain over the entire lactation period of four weeks, or expressed as fraction of the daily gain over the entire lactation:

$$Fraction = 0.583333 + 0.270833\ x\ WM - 0.058333\ xWM^2 + 0.004167\ xWM^3 \tag{15}$$

where WM = week of mortality (1; 2; 3; 4). Then mortality weight becomes:

$$Mortality\ weight, kg = birth\ weight, kg + \tag{16}$$

$$\left(\frac{Fraction \times ADG_{littermates}}{1000}\right) \times (Age\ at\ mortality, d)$$

Fat mass and protein mass of dead piglets was estimated applying Equations (13) and (14), where weaning weight was estimated as mortality weight.

Maintenance requirement of weaned piglets and those who died during lactation was estimated using the same equation as the one used for a sow (Equation (12)). Daily litter energy gain (MJ ME/d) was estimated from the fat and protein deposition of the weaned and dead piglets. Energy content of fat and protein in body tissue in piglets was assumed to be 39.5 MJ/kg fat and 23.8 MJ/kg protein.

$$Litter\ energy\ gain, MJ\ ME/d = \tag{17}$$

$$\frac{\sum_{i=1}^{n}((FM_i - (BW_i \times 0.014)) \times 39.5 + ((PM_i - (BW_i \times 0.116)) \times 23.8}{LLE_i}$$

where FM_i is fat mass (kg) at weaning of piglet i (i=1….n; n=number of weaned piglets + number of dead piglets); PM_i is protein mass (kg) at weaning; BW_i is birth weight (kg); and LLE_i = lactation length (d);

Milk energy balance

Milk energy balance, defined as the difference between milk energy output and energy required for litter gain and maintenance of piglets, should be zero. The milk energy balance can therefore be used to evaluate the described model. Milk energy comes from two sources. Of feed intake 72% of the metabolisable energy, above that needed for maintenance of the sow, was assumed to be retained as milk energy. Of body stores, 88% of the energy being mobilized can be retained as milk energy (Noblet et al., 1990). So:

Milk energy, MJ ME/d = (18)
(feed intake, kg/d × metabolisable energy in feed – maintenance of a sow) × 0.72
+ metabolisable energy from body stores × 0.88.

Furthermore, 93% of the energy in milk was assumed to be available for maintenance and growth of piglets. Energy efficiency of fat and protein deposition in piglets was assumed 78% (Mullan et al., 1993). Thus:

Energy requirement for piglets, MJ/d = (19)
[(litter energy gain / 0.78) + maintenance of the piglets] / 0.93.

3

Genetic parameters and predicted selection results for maternal traits related to lactation efficiency in sows

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Abstract

The increased productivity of sows increases the risk of a more pronounced negative energy balance during lactation. One possibility to prevent this is to increase the lactation efficiency (LE) genetically and thereby increase milk output for a given feed intake and mobilization of body tissue. The benefits of selection for LE depend on its heritability and the relationships with other traits of interest. The objectives of this study were to estimate genetic parameters for LE, its underlying traits, and to predict the consequences of current selection strategies in dam lines. Data from 4 farms were available to estimate genetic parameters. Heritabilities were estimated by using a univariate repeatability model, and genetic correlations were estimated bivariately. Selection index theory was used to predict the genetic progress by 3 alternative breeding programs: 1) a breeding program that aimed at balanced progress in the total number of piglets born, piglet mortality, and percent prolonged interval from weaning to estrus; 2) extension of this breeding goal with LE; and 3) a breeding goal that included only one selection criterion, litter weight gain, to demonstrate the effect of indirect selection for milk production. The heritability for LE was low (0.12). Body at mass (0.52) and BW (0.45) of sows at the beginning of lactation showed the greatest heritabilities. Protein mass at the beginning of lactation, protein loss, weight loss, and ad libitum feed intake during lactation showed moderate heritabilities (0.39, 0.21, 0.20, and 0.30, respectively). Low to moderate heritabilities were found for litter weight at birth, within-litter SD in the birth weight of piglets, litter weight gain, fat loss, and restricted feed intake during lactation (0.19, 0.09, 0.18, 0.05, and 0.14, respectively). Within-litter SD in the weaning weight of piglets showed no genetic variability. It was predicted that a breeding goal for dam lines with an emphasis on the total number of piglets born, piglet mortality, and percent prolonged interval from weaning to estrus would not dramatically change BW or body composition at the beginning of lactation, or mobilization of body tissue and feed intake during lactation. Inclusion of LE in the breeding goal will improve stayability, as defined by the first-litter survival of sows and LE itself, without negative consequences for other economically important traits. Nevertheless, it might be worthwhile to design a breeding goal in which LE increases and feed intake remains unchanged.

Key words: Energy balance, Genetic parameter, Lactating sow, Maternal trait

3.1 Introduction

Genetic and management changes during the last decades have increased the litter size of sows. Larger litters result in greater total suckling stimulation of the mammary glands and more suckled mammary glands (Auldist and King, 1995; Kim et al., 1999). Therefore, milk production of sows has increased during the last decades (Revell et al., 1998a). Little is known about genetic variation in milk production, because the trait is difficult to record in sows. In dairy cattle, genetic selection for milk yield alone results in increased feed intake, but also in a more pronounced negative energy balance and greater mobilization of body tissue during lactation. A large and long-lasting negative energy balance of cows generally results in reduced health and fertility (Veerkamp et al., 2001), and thus reduced stayability. Genetic studies in pigs, related to a negative energy balance, have focused on the interval from weaning to estrus (Whittemore and Morgan, 1990; Clowes et al., 2003). Selection against a prolonged interval is effective and often practiced (Ten Napel et al., 1995). How the energy balance and stayability in sows are affected by modern breeding programs is unknown. Bergsma et al. (2009) described a quantitative energetic model of lactating sows, based on on-farm observations that allows for large-scale data collection. The trait lactation efficiency was introduced and defined as the energetic efficiency of sows during lactation. Body condition score is widely used in dairy cattle to assess the body composition and energy balance status of cows (Veerkamp et al., 2001). The energetic model for lactating sows quantifies the mobilization of body tissue. The usefulness of including lactation efficiency, or its underlying traits, in a breeding program depends on its heritability and its relationships with other traits of interest. Therefore, the objectives of this study were to estimate genetic parameters for lactation efficiency and its underlying traits, and to evaluate current selection strategies in dam lines.

3.2 Materials and methods

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database. The experimental farm of IPG is strictly operating in line with the regulations of the Dutch law on protection of animals. Observations on lactating sows from 3 experiments on 4 farms were available. Traits included in calculating lactation efficiency are briefly described below. The full description of the quantitative energetic model is given by Bergsma

et al. (2009). The energy metabolism of lactating sows is given schematically in Figure 3.1.

Traits

Start weight (kg) is the BW of each sow shortly after parturition. It is estimated based on BW of the sow at transfer to the farrowing house (prepartum observation) and weight of her live and stillborn piglets at birth (postpartum observation). The assumption was made that the sow herself did not gain any BW between transfer to the farrowing house and parturition.

Body composition at the beginning of lactation of each sow [fat mass at start (kg) and protein mass at start (kg)] was estimated by using her start BW and backfat thickness. Backfat thickness was recorded ultrasonically together with BW at transfer to the farrowing house. At weaning, BW and backfat thickness of each sow were measured again. Mobilization during lactation [BW loss (kg), fat loss (kg), and protein loss (kg)] was estimated by subtracting the weight of body tissue at weaning from the corresponding weight at the beginning of lactation.
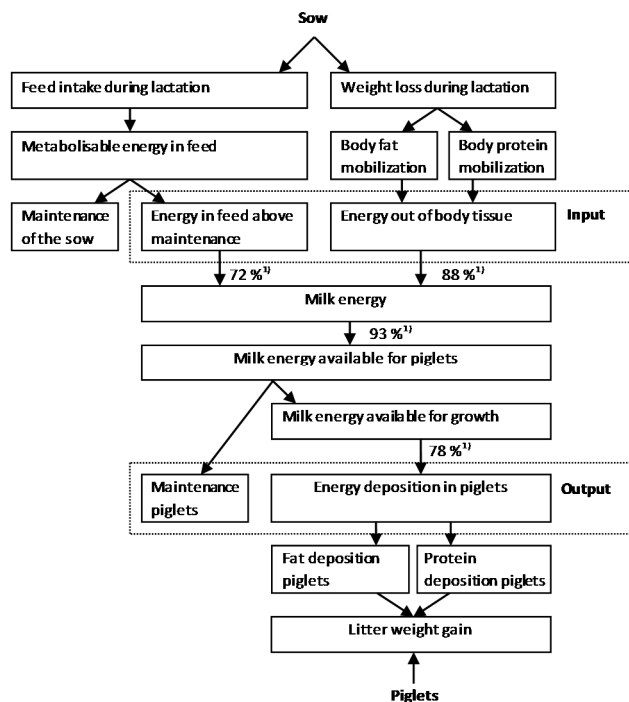
Figure 3.1 Schematic flow chart of the energy metabolism of lactating sows (Bergsma et al., 2009). [1]According to Everts and Dekker (1994).

Each sow was on a restricted diet during the first week after parturition according to an ascending scale (increased by a fixed amount each day). From wk 1 until weaning, sows were fed ad libitum [ad libitum feed intake (kg)] or restricted [restricted feed intake (kg)]. Both traits were defined as the total amount of feed consumed by each sow during lactation, including the first week.

Energy input and output were estimated per sow per day averaged over the lactation period. All energy units were expressed in megajoules of ME. Input was calculated as

Input, MJ of ME/d = (energy from total feed intake during lactation
+ energy from body fat mobilization of the sow
+ energy from body protein mobilization of the sow
− energy needed for maintenance of the sow)
÷ lactation length.

Output during lactation was calculated as:

Output, MJ of ME/d = (energy in fat deposition of live piglets at weaning
+ energy in protein deposition of live piglets at weaning
+ energy in fat deposition of dead piglets
+ energy in protein deposition of dead piglets
+ energy needed for maintenance of weaned piglets
+ energy used for maintenance of piglets that died before weaning)
÷ lactation length.

Lactation efficiency is defined as an energy efficiency of the sow, where

Lactation efficiency, % = output × 100 / input.

The greater the lactation efficiency, the greater the amount of available energy (input) that was used for piglet growth and piglet maintenance (output).

Part of the data set contained individual BW and cross-fostering recordings of piglets. In these cases, deposition of fat and protein, and the maintenance requirement of piglets were calculated from individual BW at birth and at weaning rather than litter averages. From individual piglet BW, within-litter SD of birth weight and within-litter SD of weaning weight were calculated. Within-litter SD of birth weight was calculated from individual birth weights of live born and stillborn piglets before cross-fostering, and is of interest because litters with a greater within-litter SD were found to have a greater mortality (Roehe and Kalm, 2000). Piglet BW variation within a litter at weaning is a source of concern in modern

swine management systems, because high variation delays pig movement through consecutive phases of production. Litter weight gain was calculated by subtracting the total BW of all live born piglets after cross-fostering from the total weaning weight of all weaned piglets. Litter weight at birth is the total weight of all live born and stillborn piglets before cross-fostering.

As an estimate of stayability, the trait first-litter survival of sows was introduced. Stayability is defined as the probability that an animal will stay in production until a certain age, which is an estimate of how long it will stay in production (Brigham et al., 2006). Tholen et al. (1996) studied the stayability of sows to parity 4. According to their study, the probability of a sow surviving in the herd from parity 1 to parity 2 is highly genetically correlated with the probability of the sow surviving in the herd to parity 4. The genetic correlation depends on the herd and varies from 0.75 to 0.99. First-litter survival of sows is defined as a binary trait. When a sow was bred after weaning her first litter, her first litter survival was 100%. Otherwise, her first litter survival was 0%. In our study, all gilts that were inseminated were included in this trait. Gilts that were inseminated but culled before birth of their first litter were assigned 0%.

In addition to the above-mentioned traits, 3 "traditional" traits were included in the analyses. Total number born was defined as number of live born piglets + number of stillborn piglets + number of mummified piglets. Litter mortality is the number of piglets that died during lactation as a percentage of litter size immediately after cross-fostering. Prolonged interval is 100% if a sow was inseminated at 7 d or later after weaning and 0% if a sow was inseminated at 6 d or less after weaning. In total, 19 traits were included in the analyses.

Data Sets

For all 3 experiments, all information on individual sows and their piglets was available to calculate lactation efficiency. In addition, the pedigree of each sow was known and the 3 experiments partly overlapped in pedigree.

The first experiment was described by Eissen et al. (2003) and was carried out from October 1996 until October 1998 to simulate how future high levels of litter size affect current (1997) lactating primiparous sows. This study determined whether nursing a large litter had negative effects on sow performance during lactation and postweaning. Ad libitum feed intake during lactation of each sow was recorded to evaluate whether a greater feed intake could prevent possible negative effects of large litters on sow performance, and whether selection for lactation feed intake should be recommended. This experiment was carried out on 3 farms, 1 of which was the experimental farm of IPG.

In the second data set, from the experimental farm of IPG, commercial TOPIGS crossbred sows (Vught, the Netherlands) and their offspring by different commercial sire lines were compared [R. Bergsma, E. Kanis, M. W. A. Verstegen, C. M. C. van der Peet-Schwering (Animal Sciences Group, Wageningen UR, Lelystad, the Netherlands), and E. F. Knol, unpublished data]. Since autumn 2003, BW and backfat measurement at entering and leaving the farrowing house have been implemented as a farm routine. Restricted feed intake during the stay in the farrowing house has been recorded since January 1, 2000. Individual piglet BW at birth and weaning have been recorded since September 2001, as has the recording of cross-fostering of individual piglets. Culling decisions on the experimental farm were similar to those made on commercial farms. This second data set included subsequent litters of the primiparous sows of the first data set.

The third data set was from the Sterksel experimental farm of the Animal Sciences Group of Wageningen UR. At the Sterksel farm, the effects of a low-protein and low-phosphorus gestation diet (by phase feeding) on reproductive performance, stayability, and mineral excretion were studied for 4 successive parities (van der Peet-Schwering et al., 2005). The experiments were executed from October 2000 until February 2004. During lactation, sows were fed according to an ascending scale from parturition until d 6 after parturition, and were given free access to the lactation diets from d 6 after parturition onward.

In a previous study (Bergsma et al., 2009), phenotypic correlations between lactation efficiency and its underlying traits, and phenotypic correlations between lactation efficiency and traditional reproductive traits were remarkably similar (results not shown) for 2 farms, even though 1 farm fed sows ad libitum during lactation and the other fed a restricted diet. Therefore, observations in the above-mentioned 3 experiments were treated as 1 data set.

Creep feed was offered (but feed intake was not recorded) to piglets before weaning during the second and third experiment and was not offered to piglets throughout the lactation during the first experiment. Lactation efficiency therefore did not include feed intake by piglets. When creep feed was provided to the piglets, intake was estimated at 200 to 300 g per piglet during a 4-wk lactation. On all 4 farms, a commercial lactation diet was fed to sows during lactation.

To complete the data set, information on all 4 farms regarding reproductive traits, from September 1, 1996, onward, was added. The number of observations per trait varied considerably (Table 3.1).

Table 3.1 Number of observations, mean, phenotypic SD (σ), heritability (h^2), and repeatability (r^2) by trait (SE in parentheses).

Item	No. obs.	Mean	$\sigma_{phenotypic}$ [1]	h^2	r^2
Total number born, n	19,759	12.56	3.13	0.13 (0.02)	0.22 (0.01)
Litter mortality, %	18,718	11.7	12.4	0.04 (0.01)	0.09 (0.01)
Prolonged interval percent	15,844	13.0	31.3	0.08 (0.01)	0.11 (0.01)
First-litter survival of sows, %	4,261	85.1	33.6	0.05 (0.02)	-
Start BW, kg	2,063	203	15.7	0.45 (0.08)	0.54 (0.03)
Fat mass at start, kg	2,044	43.3	6.9	0.52 (0.08)	0.57 (0.03)
Protein mass at start, kg	2,044	31.2	2.4	0.39 (0.08)	0.59 (0.03)
Litter weight at birth, kg	2,629	17.2	3.8	0.19 (0.05)	0.29 (0.03)
SD birth weight, g	1,465	286	88	0.09 (0.05)	0.10 (0.03)
Ad libitum feed intake, kg [2]	1,101	116.8	19.0	0.30 (0.08)	0.34 (0.07)
Restricted feed intake, kg [2]	2,113	142.3	17.7	0.14 (0.05)	0.23 (0.03)
BW losses, kg	1,973	18.7	13.0	0.20 (0.06)	0.23 (0.03)
Fat losses, kg	1,952	8.8	4.5	0.05 (0.04)	0.14 (0.03)
Protein losses, kg	1,952	2.1	2.0	0.21 (0.06)	0.21 (0.03)
Litter weight gain, kg	2,560	62.3	10.3	0.18 (0.05)	0.27 (0.03)
SD weaning weight, g	1,482	1,356	471	0.00 (0.03)	0.11 (0.03)
Input, MJ/d	1,883	58.4	10.0	0.15 (0.06)	0.26 (0.03)
Output, MJ/d	2,562	38.8	6.1	0.17 (0.05)	0.25 (0.03)
Lactation efficiency, %	1,857	66	10.6	0.12 (0.03)	0.12 (0.03)

[1] Phenotypic SD were adapted from ASREML analyses: $\sqrt{\sigma^2_{animal} + \sigma^2_{permanentenvironment} + \sigma^2_{error}}$;

[2] Total feed intake during lactation.

Estimation of Genetic Parameters

Genetic parameters were estimated by using REML analyses based on an animal model. A repeatability model was used for all traits except for the first-litter survival of sows. The mixed model can be written as **y = Xb + Za + Wc + e**, where **y** is the vector of observations; **X**, **Z**, and **W** are known incidence matrices; **b** is the solution vector of fixed effects; **a** is the vector of random additive genetic effects $\sim N(\mathbf{0}, A\sigma^2_a)$; **c** is the vector of random permanent nongenetic effects of each sow $\sim N(\mathbf{0}, I_c\sigma^2_c)$; and **e** is the vector of the residuals $\sim N(\mathbf{0}, I_e\sigma^2_e)$. I_c and I_e are identity matrices, and **A** is the additive genetic relationship matrix. The term **Wc** was included only in the repeatability models. Analyses were performed with ASREML software (Gilmour et al., 2002).

The pedigree matrix contained 3 generations of parents. In total, 8,469 animals were included in the pedigree matrix. The 4,687 sows with performance records for total number born were descended from 492 sires and 1,222 dams. The 1,088 sows

with performance records for lactation efficiency descended from 172 sires and 480 dams.

Genetic parameters were estimated in 2 ways. Univariate analyses were performed to estimate the heritability and repeatability of lactation efficiency, its underlying components, and some reproductive traits. Bivariate analyses were performed to estimate the genetic and phenotypic co variances between traits. To obtain the maximum accuracy of estimates, different statistical models were used for different traits. The fixed effects included in the vector b are given in models (a) through (g) (Table 3.2). Only significant effects were included in the models. Effects for which heritabilities were estimated were excluded from the models in both univariate and bivariate analyses.

Table 3.2 Fixed effects included in the vector **b** for different traits.

Model	Trait fixed effects [1]
(a)	Fat mass at start; protein mass at start; BW at start
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l$
(b)	Fat loss; protein loss; BW loss; ad libitum feed intake; restricted feed intake; lactation efficiency; litter weight gain; input; output
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l + b_1 \times \text{LLE}$
(c)	Litter weight at birth; within-litter SD in birth weight; within-litter SD in weaning weight
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l + \text{LINE} \male_m + \text{LINE} \female_l \times \text{LINE} \male_m$
(d)	Litter mortality
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l + \text{LINE} \male_m + \text{LINE} \female_l \times \text{LINE} \male_m + b_1 \times \text{LLE}$
(e)	Total number born
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l + \text{LINE} \male_m + \text{LINE} \female_l \times \text{LINE} \male_m + \text{DI}_n + \text{REMAT}_o$
(f)	Prolonged interval percent
	$\mu + \text{PARITY}_j + \text{HYS}_k + \text{LINE} \female_l + b_1 \times \text{LLE} + b_2 \times \text{LLE}^2 + b_3 \times \text{NOWND}$
(g)	First-litter survival of sows
	$\mu + \text{HYS2}_j + \text{LINE} \female_k + b_1 \times \text{AFI}$

[1] Where μ = population mean; PARITY = the parity of the sow (parity 6 and greater were combined); HYS = herd-year-season = farm × month of farrowing, where HYS accounts for differences between experiments; LINE $\female$ = the line code of the sow; LINE $\male$ = the line code of the father of the litter; DI = double insemination, whether (1) or not (0) the sow was bred more than once within the same cycle; REMAT = remating, whether (0) or not (1) the present litter originated from the first insemination after weaning (multiparous sows) or rearing (primiparous sows; apart from double insemination); LLE = length of lactation, d; NOWND = number of piglets weaned (n); HYS2 = farm × quarter of insemination (herd-year-season); AFI = age at first breeding, d.

SelAction

To predict the consequences of a modern breeding program on lactation efficiency, its underlying components, and some reproductive traits, the simulation program SelAction was used (Rutten et al., 2002). SelAction predicts the genetic progress in a breeding program, and thereby gives a better understanding of the biological mechanism of energy metabolism of lactating sows.

SelAction predicts genetic gain by using an accurate approximation of a stochastic simulation, with selection on BLUP-EBV from an animal model. A population with discrete generations and a fixed number of sires and dams was simulated. In SelAction, animals are assumed to be selected on an index (I) that equals their expected value for the aggregate genotype. This corresponds to an index as used in practice:

$$I = EW_{trait_1} \times EBV_{trait_1} + EW_{trait_2} \times EBV_{trait_2} + \cdots + EW_{trait_n} \times EBV_{trait_n},$$

where EW is the economic weight.

Genetic gain was simulated for 3 dam-line breeding goals:

1. A breeding goal with 3 traits: total number born, litter mortality, and percent prolonged interval from weaning to estrus. Economic values (Table 3.3) were chosen in such a way that, according to SelAction, 50% of the selection response was due to improvement of the total number born, 25% to litter mortality, and 25% to a prolonged interval from weaning to estrus.

Table 3.3 Relative economic values, phenotypic variance (σ^2 phenotypic), and heritability (h^2) for traits included in the selection index of the 3 alternative breeding programs {models (1) to (3)}.

			Relative economic value		
Trait	$\sigma^2_{phenotypic}$	h^2	(1) Balanced	(2) Balanced including lactation efficiency	(3) Litter weight gain
Total number born, n	9.82	0.13	1.0000	1.0000	-
Litter mortality, %	153.9	0.04	-0.4665	-0.4665	-
Prolonged interval percent	981.2	0.08	-0.0683	-0.0683	-
Lactation efficiency, %	112.7	0.12	-	1.0000	-
Litter weight gain, kg	14.54	0.19	-	-	1.0000

2. A breeding goal with lactation efficiency, together with the traits from simulation 1, total number born, litter mortality, and percent prolonged interval from weaning to estrus. The economic values for lactation efficiency and total number born were assumed to be equal.

3. A breeding goal with litter weight gain. The latter simulation was used to demonstrate the effect of indirect selection for milk production.

To model the breeding program, the following assumptions were made:

• There was an active population of 5,000 sows, with an annual replacement of 40%;
• 40 sires were used every year;
• 10% of the litters produced were purebred litters for which only second-parity sows were used;
• Each sow produced 2.35 litters per year;
• Per purebred litter, 3.5 female piglets and 2.1 male piglets were reared;
• A 2-stage-selection was simulated:
   o At the end of the rearing period (at approximately puberty) BLUP-EBV selection for young boars and sows was performed; and
   o After the first litter, sows were selected to produce a purebred litter based on BLUP-EBV, including their own performance, plus the performance of full sibs, plus the performance of half sibs. No second selection step was included for boars;
• Piglets that were not reared were excluded for reasons other than the breeding goal;
• After the rearing period, 40% of the males and 85% of the females were available for selection; the remaining 60% of the males and 15% of the females were excluded from breeding for reasons other than the breeding goal;
• 85% of the first-litter sows produced a second litter. The remaining 15% were excluded for reasons other than the breeding goal; and
• The maximum number of offspring selected per dam was 1 male and 3.5 females.

These assumptions resulted in a "proportion of selected male parents" of 0.041 and a "proportion of selected female parents" of 0.395. The length of the generation interval was 15 mo.

The second stage of selection in sows was based on BLUP-EBV, including their own performance and the performance of full and half sibs. Simulation 1 implied

observations on the total number born, litter mortality, and percent prolonged interval from weaning to estrus. Additionally, simulation 3 included observations on litter weight gain. Simulation 2 included observations on all traits. For SelAction, the underlying traits of lactation efficiency are not necessary. Because they are needed to estimate lactation efficiency and are thus available, they were assumed to be used in the simulation as well. An accurate estimation of lactation efficiency requires individual BW of piglets. Observations on traits other than underlying traits of lactation efficiency that could be calculated from the individual piglets' BW, such as within-litter SD for birth weight and litter weight at start, were assumed to be available as well.

Phenotypic variances and heritabilities needed in SelAction were obtained from the univariate analyses. Phenotypic and genetic correlations were obtained from bivariate analyses.

3.3 Results

Unadjusted means and numbers of observations for all traits are presented in Table 3.1. Ad libitum feed intake showed a lower average than restricted feed intake. The group of sows fed ad libitum during lactation contained a relatively large number of primiparous sows. Observations on restricted feed intake came from the experimental farm of IPG (data set 2). The realized feed intake on that farm was relatively high compared with other farms (Bergsma et al., 2009).

Heritabilities
Estimates of heritabilities and repeatabilities are also given in Table 3.1. Body weight and body composition traits at the beginning of lactation showed the greatest heritabilities. Apart from the direct genetic effect, there was a nongenetic permanent environmental effect for these traits, with repeatabilities from 0.54 to 0.59. Of these 3 traits, fat mass at the beginning of lactation showed the greatest heritability. Of the body tissue losses, fat loss showed a relatively low heritability of 0.05, whereas weight and protein losses showed a heritability of 0.20 and 0.21, respectively. Heritability for ad libitum feed intake was 0.30 and for restricted feed intake was 0.14. Repeatabilities for these intake traits were more similar, 0.34 and 0.23, respectively. The SE of the estimate for the heritability of ad libitum feed intake was relatively high (0.08) because of the low number of observations. Lactation efficiency showed a heritability of 0.12. No nongenetic permanent environmental effect was found for lactation efficiency, because heritability and repeatability both yielded 0.12. The heritability for first-litter survival of sows was

0.05. This is in line with findings by Tholen et al. (1996). For 2 different herds, they found a heritability of 0.05 and 0.02, respectively, with a corresponding genetic variance of 60 and 34%, respectively. The genetic variance in our study was 60.5%, although definitions differed slightly. The heritabilities for litter weight at birth, litter weight gain, input, and output varied from 0.15 to 0.19, and the repeatabilities varied from 0.25 to 0.29. The within-litter SD of birth weight showed a heritability of 0.09 and a repeatability of 0.10. The repeatability for within-litter SD in weaning weight was similar: 0.11. However, no genetic variance was found for this trait. Heritabilities for the more traditional traits such as total number born, litter mortality, and percent prolonged interval were in line with the literature (Rothschild and Bidanel, 1998).

Genetic Correlations

Results of the bivariate analyses are shown in Table 3.4. Within-litter SD in weaning weight showed no additive genetic variance and were therefore excluded from the bivariate analyses.

The genetic correlation between total number of born piglets and litter mortality was +0.39 (Table 3.4). A positive genetic correlation between total number born and litter mortality has been reported frequently (Rothschild and Bidanel, 1998). Most other genetic correlations with the total number born are rather small. Litter weight at birth, litter weight gain, and thus output increase genetically with greater litter sizes. The genetic correlation of litter weight gain and litter mortality was negative (−0.43) and thus favorable. Within-litter SD in birth weight increased with increasing litter size, although not significantly. Our study, as well as the one by Knol (2001), showed no significant genetic correlation of within-litter SD in birth weight with total number born.

Sows with a high genetic merit for ad libitum feed intake showed (genetically) lower weight, fat, and protein losses during lactation. The input was still greater compared with sows with a low genetic merit for ad libitum feed intake. A high genetic merit for ad libitum feed intake yielded (genetically) a greater litter weight gain and thus a greater output. There were some unexpected differences between ad libitum feed intake and restricted feed intake. In general, the genetic correlations were stronger with ad libitum feed intake than with restricted feed intake. The genetic correlations of feed intake with litter mortality and lactation efficiency were the exceptions. Some of the correlations were of different signs; however, in these cases such correlations were not significantly different from

Table 3.4 Genetic correlations above the diagonal, phenotypic correlations below the diagonal (SE in parentheses); bold printed correlations differ from zero (P<0.05)[1].

Item	TNB	LMO	PINT	1LS	WTS	FMS	PMS	LWTB	SDBW	ALFI	RFI	WTL	FL	PL	LWG	IN	OUT	LE
TNB	–	**+0.39** (0.10)	-0.06 (0.10)	+0.12 (0.15)	-0.15 (0.13)	-0.27 (0.12)	-0.05 (0.14)	**+0.78** (0.06)	+0.45 (0.29)	+0.01 (0.17)	-0.04 (0.25)	0.00 (0.17)	-0.11 (0.28)	-0.01 (0.17)	**+0.45** (0.16)	+0.26 (0.20)	**+0.46** (0.17)	-0.09 (0.14)
LMO	**+0.23** (0.01)	–	+0.09 (0.13)	-0.20 (0.18)	-0.07 (0.16)	-0.13 (0.15)	-0.02 (0.17)	-0.23 (0.20)	-0.35 (0.43)	-0.05 (0.20)	**-0.59** (0.27)	-0.10 (0.20)	-0.34 (0.31)	-0.09 (0.20)	**-0.43** (0.18)	-0.27 (0.22)	**-0.48** (0.18)	-0.24 (0.19)
PINT	+0.00 (0.01)	+0.00 (0.01)	–	-0.14 (0.18)	-0.24 (0.15)	-0.20 (0.14)	+0.23 (0.16)	-0.14 (0.19)	**+0.88** (0.26)	+0.18 (0.20)	-0.19 (0.28)	+0.02 (0.19)	+0.22 (0.30)	-0.04 (0.19)	+0.15 (0.20)	+0.05 (0.23)	+0.15 (0.20)	+0.10 (0.17)
1LS	-0.04 (0.01)	-0.04 (0.02)	+0.01 (0.02)	–	**+0.50** (0.18)	**+0.39** (0.19)	**+0.44** (0.20)	+0.32 (0.26)	**-0.92** (0.40)	**-0.60** (0.26)	**-0.92** (0.33)	-0.29 (0.27)	+0.43 (0.42)	-0.04 (0.25)	-0.23 (0.27)	-0.34 (0.33)	-0.20 (0.27)	+0.30 (0.34)
WTS	**-0.11** (0.02)	-0.01 (0.02)	-0.00 (0.02)	+0.07 (0.04)	–	**+0.63** (0.02)	**-0.93** (0.00)	-0.09 (0.19)	-0.68 (0.21)	-0.18 (0.18)	-0.43 (0.24)	-0.27 (0.17)	-0.25 (0.29)	-0.29 (0.17)	-0.08 (0.18)	-0.27 (0.20)	-0.13 (0.19)	**+0.25** (0.12)
FMS	**+0.11** (0.02)	**-0.05** (0.02)	-0.02 (0.02)	**+0.11** (0.04)	**+0.63** (0.02)	–	+0.39 (0.12)	-0.36 (0.16)	-0.20 (0.28)	-0.03 (0.19)	-0.08 (0.23)	-0.21 (0.17)	-0.10 (0.26)	-0.25 (0.17)	-0.13 (0.17)	-0.12 (0.20)	-0.14 (0.18)	-0.09 (0.11)
PMS	**-0.08** (0.02)	+0.01 (0.02)	+0.01 (0.02)	+0.03 (0.04)	**-0.93** (0.00)	+0.32 (0.03)	–	-0.03 (0.18)	+0.32 (0.30)	+0.20 (0.19)	-0.48 (0.26)	-0.19 (0.18)	-0.35 (0.30)	-0.19 (0.18)	-0.04 (0.19)	-0.25 (0.20)	-0.10 (0.19)	**+0.36** (0.12)
LWTB	**+0.80** (0.01)	**+0.06** (0.02)	+0.03 (0.02)	-0.03 (0.04)	-0.09 (0.03)	-0.09 (0.03)	-0.06 (0.03)	–	+0.12 (0.03)	+0.08 (0.04)	+0.02 (0.03)	+0.56 (0.19)	-0.56 (0.30)	-0.05 (0.40)	+0.29 (0.21)	+0.30 (0.23)	-0.39 (0.21)	-0.03 (0.15)
SDBW	**+0.11** (0.03)	-0.04 (0.03)	-0.03 (0.03)	-0.06 (0.07)	-0.02 (0.04)	-0.02 (0.04)	-0.00 (0.04)	**+0.12** (0.03)	–	-0.20 (0.28)	-0.14 (0.39)	-0.19 (0.41)	-0.25 (0.51)	-0.05 (0.40)	-0.09 (0.37)	-0.50 (0.35)	-0.14 (0.35)	-0.51 (0.36)
ALFI	**+0.07** (0.03)	-0.04 (0.03)	-0.02 (0.03)	**-0.15** (0.04)	-0.24 (0.04)	-0.15 (0.04)	+0.22 (0.04)	+0.08 (0.04)	-0.20 (0.28)	–	-0.27 (0.10)	-0.40 (0.10)	-0.37 (0.03)	-0.38 (0.03)	-0.37 (0.03)	**+0.83** (0.11)	**+0.42** (0.21)	-0.38 (0.20)
RFI	+0.04 (0.02)	**-0.11** (0.02)	**-0.08** (0.03)	-0.10 (0.06)	**-0.11** (0.04)	-0.13 (0.04)	-0.08 (0.04)	+0.02 (0.03)	+0.03 (0.03)	-0.27 (0.10)	–	-0.18 (0.04)	-0.25 (0.51)	-0.32 (0.30)	-0.09 (0.37)	**+0.99** (0.12)	+0.41 (0.26)	**-0.74** (0.19)
WTL	**-0.11** (0.03)	**-0.27** (0.02)	-0.03 (0.03)	**-0.18** (0.04)	**-0.24** (0.04)	+0.16 (0.04)	+0.22 (0.04)	-0.03 (0.03)	-0.05 (0.04)	-0.40 (0.10)	-0.27 (0.04)	–	-0.67 (0.01)	**-0.96** (0.00)	-0.86 (0.12)	-0.39 (0.02)	-0.31 (0.20)	+0.08 (0.16)
FL	**-0.05** (0.03)	**-0.29** (0.02)	-0.02 (0.02)	**-0.12** (0.04)	-0.10 (0.03)	**-0.36** (0.02)	-0.04 (0.03)	-0.11 (0.03)	-0.02 (0.04)	-0.37 (0.03)	-0.18 (0.04)	**-0.67** (0.01)	–	**-0.80** (0.16)	-0.04 (0.20)	-0.18 (0.40)	-0.09 (0.36)	-0.18 (0.23)
PL	**-0.12** (0.03)	**-0.23** (0.02)	+0.02 (0.02)	**-0.12** (0.04)	**+0.25** (0.03)	+0.06 (0.03)	**+0.28** (0.03)	-0.01 (0.03)	+0.06 (0.04)	-0.38 (0.03)	-0.25 (0.30)	**-0.96** (0.00)	-0.32 (0.30)	–	+0.33 (0.20)	+0.02 (0.25)	+0.37 (0.19)	-0.14 (0.16)
LWG	**+0.05** (0.02)	**-0.36** (0.02)	-0.02 (0.02)	-0.02 (0.04)	-0.02 (0.03)	+0.00 (0.03)	+0.03 (0.03)	**+0.14** (0.02)	-0.01 (0.04)	-0.37 (0.03)	+0.31 (0.03)	-0.86 (0.02)	+0.44 (0.02)	+0.31 (0.02)	–	**-0.68** (0.14)	**+0.99** (0.00)	+0.23 (0.15)
IN	-0.01 (0.03)	**-0.29** (0.02)	-0.01 (0.02)	-0.03 (0.04)	-0.04 (0.03)	+0.10 (0.03)	-0.09 (0.03)	**+0.13** (0.03)	-0.05 (0.04)	**-0.69** (0.02)	**-0.59** (0.02)	-0.36 (0.02)	-0.54 (0.02)	-0.24 (0.03)	+0.60 (0.02)	–	+0.69 (0.14)	-0.55 (0.02)
OUT	-0.00 (0.02)	**-0.42** (0.02)	-0.01 (0.02)	-0.01 (0.04)	+0.02 (0.03)	-0.00 (0.03)	+0.02 (0.03)	+0.03 (0.02)	-0.00 (0.03)	-0.37 (0.03)	-0.33 (0.03)	-0.39 (0.02)	-0.35 (0.02)	+0.35 (0.02)	**+0.99** (0.00)	**+0.61** (0.02)	–	-0.31 (0.02)
LE	+0.05 (0.03)	-0.09 (0.02)	-0.00 (0.02)	+0.00 (0.04)	+0.07 (0.03)	-0.10 (0.03)	+0.13 (0.03)	+0.03 (0.03)	-0.07 (0.04)	-0.44 (0.03)	-0.36 (0.03)	-0.03 (0.03)	-0.26 (0.02)	+0.06 (0.03)	+0.31 (0.02)	-0.55 (0.02)	**-0.31** (0.02)	–

1) TNB = total number born, n; LMO = litter mortality, %; PINT = prolonged interval percent; 1LS = first-litter survival of sows, %; WTS = start weight, kg; FMS = fat mass at start, kg; PMS = protein mass at start, kg; LWTB = litter weight at birth, kg; SDBW = SD of birth weight, kg; ALFI = ad libitum feed intake, g; RFI = restricted feed intake, kg; WTL = weight loss, kg; FL = fat loss, kg; PL = protein loss, kg; LWG = litter weight gain, kg; IN = input, MJ/d; OUT = output, MJ/d; LE = lactation efficiency, %.

zero. The genetic correlation between ad libitum feed intake and restricted feed intake was high but not significantly different from zero. The high SE of this genetic correlation is the result of lacking common observations. Genetic correlations were mainly based on family information, only a few sows were fed ad libitum during their first lactation and fed restricted during subsequent lactations. Ad libitum feed intake and within-litter SD in birth weight also lacked common observations. Therefore, the estimated genetic correlation of +0.97 did not differ significantly from zero. High ad libitum feed intake was unfavorable for stayability, as defined by the first-litter survival of sows ($r_g = -0.60$), as was a high restricted feed intake ($r_g = -0.92$).

A high genetic merit for stayability seemed to be associated with a high genetic merit for gain (fat, protein, or both) because of the rather high genetic correlation of first-litter survival of sows with weight, fat mass, and protein mass at the beginning of lactation. The phenotypic correlations between these traits were rather small. A genetically greater protein mass and, as a result, a greater weight at the beginning of the lactation were genetically associated with a lower within-litter SD in birth weight. The (strong) negative genetic correlation between first-litter survival of sows and within-litter SD in birth weight probably goes along the pathway of development, because start weight was genetically positively correlated with first-litter survival and strongly negatively correlated with within-litter SD in birth weight. Surprisingly, the phenotypic correlation between first-litter survival of sows and within-litter SD in birth weight did not differ from zero. Within-litter SD in birth weight also showed strong positive genetic correlations with prolonged interval and fat loss during lactation. This suggests that a low within-litter SD in birth weight is a preferable characteristic, although we found no (phenotypic or genetic) correlation between within-litter SD in birth weight and litter mortality.

A (genetically) high fat mass at the beginning of lactation was associated with a reduced litter size and a lower litter weight at birth. When sows are fed according to a scheme during gestation and the number of fetuses is low, more energy will be available for deposition of fat at the end of gestation. This is a phenotypic relation, but this phenomenon may have affected the estimates of the genetic correlation. Losses during lactation (weight, fat, or protein) are genetically strongly associated, as are the different components of weight at the beginning of lactation. (Genetically) high weight and protein mass at the beginning of lactation and low input as a result of low restricted feed intake are favorably associated with lactation efficiency.

There are, in general, no significant phenotypic correlations between percent prolonged interval and any other trait. This was unexpected because positive correlations between fat loss and, in particular, protein loss and a prolonged interval have been reported frequently (Whittemore and Morgan, 1990; Clowes et al., 2003).

Simulations

Predicted responses for the 3 breeding goals are given per generation in Table 3.5. The length of the generation interval was 15 mo in each simulated breeding program.

The first breeding goal yielded balanced genetic progress: improvement of all 3 traits involved. Selection for the total number born, litter mortality, and percent prolonged interval yielded an increased first-litter survival of sows of 0.6% per generation as a correlated response. Litter weight gain (and thus output) increased, as did litter weight at birth and restricted feed intake. Ad libitum feed intake did not. Changes in body tissue losses during lactation were rather small (less than 3% of the genetic SD). Small changes in the underlying components caused input to increase. Output and input both increased by 0.4 MJ/d of lactation per generation, which means sows became (genetically) more efficient. Output and input increased with the same magnitude, and because the level of input was greater than the level of output, lactation efficiency also improved genetically. Body weight and fat mass at the beginning of lactation seemed to decrease slightly (5% of the genetic SD for start weight and 6% for fat mass at the beginning of lactation). Uniformity at birth hardly changed. The within-litter SD in birth weight increased by 1 g per generation, which was less than 4% of the genetic SD.

Inclusion of lactation efficiency in the breeding goal barely affected absolute improvement of the total number born, litter mortality, and percent prolonged interval. Additionally, lactation efficiency increased by 1% per generation instead of 0.2% when applying the balanced breeding goal. Efficiency increased because input decreased and output increased. Feed intake (restricted and ad libitum) decreased but mobilization of body tissue increased. Litter weight gain increased by 0.8 kg per generation. Sows became leaner at the beginning of lactation because weight increased and fat mass decreased. Changes in first-litter survival of sows, within SD in birth weight and litter weight at birth, were rather large (52, 23, and 42% of their genetic SD, respectively).

Selection for lactation efficiency implied data collection for all traits. As a consequence of extra observations, the accuracy of the selection index increased. For the balanced breeding goal with observations on the total number born, litter

Table 3.5 Selection responses and correlated responses of simulations with SelAction[1].

Trait	Model					
	(1) Balanced		(2) Balanced including lactation efficiency		(3) Litter weight gain	
	Trait units	% of total response	Trait units	% of total response	Trait units	% of total response
Total number born, n	+0.19	50	+0.21	31	+0.20	
Litter mortality, %	-0.2	25	-0.3	22	-0.3	
Prolonged interval percent	-1.4	25	-1.2	11	+0.5	
First-litter survival of sows, %	+0.6		+3.9		-0.5	
Start BW, kg	-0.6		+0.1		-0.3	
Fat mass at start, kg	-0.3		-0.4		-0.2	
Protein mass at start, kg	-0.1		+0.1		-0.0	
Litter weight at birth, kg	+0.3		+0.7		+0.2	
SD birth weight, g	+1		-6		+0	
Ad libitum feed intake, kg	-0.1		-0.4		+1.6	
Restricted feed intake, kg	+0.8		-0.4		+0.6	
BW loss, kg	+0.1		+0.4		+0.5	
Fat loss, kg	+0.0		+0.1		+0.0	
Protein loss, kg	+0.0		+0.2		+0.1	
Litter weight gain, kg	+0.6		+0.8		+1.4	100
Input, MJ/d	+0.4		-0.4		+0.9	
Output, MJ/d	+0.4		+0.3		+0.8	
Lactation efficiency, %	+0.2		+1.0	36	+0.3	

[1] Rutten et al. (2002).

mortality, and percent prolonged interval, the accuracy of the index was 0.418 for females and 0.119 for males according to SelAction. When we included observations on all (18) traits, the accuracy increased to 0.602 for females and 0.181 for males (results not shown).

Selection for litter weight gain only yielded an increased percent prolonged interval from weaning to estrus, increased ad libitum feed intake, increased restricted feed intake, and decreased stayability. The reductions in start weight and fat mass were less severe compared with the genetic progress simulated with the balanced breeding goal. On the other hand, weight loss during lactation, but not fat loss, increased absolutely and relatively to the balanced breeding goal. Obviously, litter weight gain as well as output showed greater genetic progress while simulating a breeding goal with litter weight gain only. As a consequence of increased feed intake and mobilization of body tissue, input also increased.

The breeding goal with litter weight gain only yielded greater genetic progress for the total number born and litter mortality than did the balanced breeding goal.

Selection for litter weight gain implied data collection for that trait. The genetic correlations between litter weight gain, on one hand, and total number born and litter mortality, on the other hand, were moderate (0.45 and 0.43, respectively). As a consequence of extra observations for genetically correlated traits, the accuracy of the BLUB-EBV for the total number born and litter mortality increased, compared with the breeding goal without observations on litter weight gain.

3.4 Discussion

Heritabilities

Body weight and body composition, especially fat mass at the beginning of lactation, showed high heritabilities (0.4 to 0.5). Mobilization of body tissue during lactation was not as heritable as body composition at the beginning of the lactation. Fat loss during lactation showed a low heritability of 0.05. Grandinson et al. (2005) estimated a heritability for sow BW within 1 d of parturition of 0.19, and 0.47 for the corresponding ultrasonic backfat thickness. For BW loss and backfat loss during lactation, they found heritabilities of 0.20 and 0.10, respectively. Estimates of heritability for backfat thickness, backfat loss, and BW loss in the current study and in the study by Grandinson et al. (2005) were very similar. Estimated heritability of BW at the beginning of lactation was greater in our study (0.45) than in the study by Grandinson et al. (2005; 0.19). Fat mass in our study was based on BW and ultrasonic backfat thickness, and therefore fat mass and ultrasonic backfat thickness are different, but related, expressions of fat deposition. Thus, an equal heritability might be expected.

The high heritabilities of BW and fat mass at the beginning of lactation are unexpected because farm management aims to prevent variation in BW and body condition scores between sows at parturition. Nevertheless, sows apparently managed to express their own genetic potential. Preventing variation means that farmers expect a phenotypic optimum for BW and backfat thickness at the beginning of lactation. This is not unreasonable because, for example, body fat at the beginning of lactation and feed intake during lactation are negatively correlated (Revell et al., 1998). Therefore, breeding values for BW and fat mass at the beginning of lactation could be a useful tool to determine the optimum feeding scheme during gestation for individual sows.

The heritability of litter weight at birth was high in our experiments (0.19) compared with that of Roehe (1999), who reported a heritability of 0.08 (±0.03)

without adjustment for litter size at birth. However, in another model in which birth weight was regarded as a trait of an individual (live born) pig, which was influenced by a direct genetic effect and a maternal genetic effect, the maternal component was 0.26 (±0.04). The maternal heritability of individual birth weight may be expected to be equal to the heritability of litter weight at birth (Roehe, 1999). Rothschild and Bidanel (1998) reported a mean heritability from the literature of 0.29 for litter weight at birth. In their review, they reported a heritability of 0.17 for litter weight at 21 d of age. Damgaard et al. (2003) found a heritability of 0.19 for mean BW at 3 wk of age. The trait litter weight at 21 d or mean BW at 3 wk of age was influenced by birth weight of the piglets. No literature was found for heritability of litter weight gain to compare with our estimate (0.18). If litter weight gain is a reflection of milk yield (Revell et al., 1998a), its heritability can be compared with heritability estimates for milk yield in dairy cattle. Veerkamp (1998) reviewed research in this area. The average estimate was 0.32, and estimates varied from 0.16 to 0.50.

Litter weight gain and output were genetically the same traits (r_g = +0.99). This was expected because both traits were derived from BW of piglets at birth and at weaning within a litter.

Knol (2001) reported a heritability of 0.07 ±0.01 for the within-litter SD in birth weight. Heritability in our experiment was somewhat greater. The within-litter SD of weaning weight showed no additive genetic variance in our study. Damgaard et al. (2003) reported a heritability of 0.06 ± ⬚0.03 for the within-litter SD of BW at 3 wk of age. They reported a heritability of 0.08 ± 0.03 for the within-litter SD in birth weight of live born piglets, and a genetic correlation of 0.71 ± ⬚0.21 between within-litter SD at birth and at weaning. Contrary to our experiments, cross-fostering was not practiced by Damgaard et al. (2003). One of the reasons for cross-fostering is to reduce the within-litter SD in BW. From the results of our study and those of Damgaard et al. (2003), we can conclude that the within-litter SD in weaning weight showed no additive genetic variance. In situations in which no cross-fostering was practiced, within-litter SD in weaning weight was an expression of within-litter SD in birth weight. The latter trait showed a heritability of 0.09.

No literature was found to compare with our estimate of heritability for lactation efficiency. The trait in finishing pigs that comes nearest to the lactation efficiency of sows is residual feed intake. The reported heritabilities have varied from 0.10 to 0.45 (de Haer, 1992; Johnson et al., 1999; Nguyen et al., 2005). Heritability of lactation efficiency (0.12) was at the lower bound of these estimates. Lactation efficiency was considered as a trait of the sow but is also influenced by the feed conversion capacity of the individual piglets, which might have resulted in a lower

estimate of the heritability. The heritability was low but significantly larger than zero, suggesting that genetic improvement of lactation efficiency by selection can be successful.

Genetic Correlations

Genetic correlations among the total number born, litter mortality, and litter weight at birth from our study were in line with those reported by Rothschild and Bidanel (1998). Our data set appeared to be a representative sample, which was also supported by our findings on heritabilities.

Eissen et al. (2003) suggested increasing the feed intake capacity of sows to facilitate sows to wean larger litters. For most characteristics, a greater genetic merit for feed intake is favorable. Increased feed intake during lactation is associated with decreased BW, fat, and protein losses during lactation and with increased litter weight gain. Feed intake (ad libitum and restricted), in contrast, seems not to affect the percent prolonged interval from weaning to estrus, which was unexpected. There was only a small (but significant) negative phenotypic correlation between restricted feed intake and percent prolonged interval. High ad libitum feed intake was unfavorable for first-litter survival (r_g = −0.60), and so was high restricted feed intake (r_g = −0.92). Our genetic correlations had a rather large SE (0.26 and 0.33, respectively); however, the statistical chances that they were at least moderately negative were large. Unfortunately, we lack a biological interpretation of this negative correlation. A possible explanation for this phenomenon found in the literature was provided by Tolkamp and Ketelaars (1992): increased feed intake will lead to increased oxygen intake. Consumption of oxygen has damaging effects on living organisms, because it accumulates in the course of life and results in a loss of vitality, aging, and finally death. Our phenotypic correlation between feed intake and first-litter survival, on the other hand, was positive (ad libitum feed intake), which was supported by negative phenotypic correlations between BW loss, fat loss, and protein loss during lactation and first-litter survival. Our phenotypic relations are in line with Serenius et al. (2006), who stated that sows with lower feed intake and greater backfat loss during lactation had a shorter productive lifetime. Tholen et al. (1996) and López-Serrano et al. (2000) studied the genetic correlation between stayability of sows from the first to the second parity and finishing traits (daily gain and backfat thickness). These studies showed an average genetic correlation between daily gain and stayability of −0.2, and a genetic correlation of +0.2 between backfat thickness and stayability. Cassady et al. (2004) found that offspring of a maternal line superior in sow longevity grew slower and had poorer carcass composition than offspring from

5 other maternal lines studied. Clutter and Brascamp (1998) showed that the genetic correlation between daily gain and feed intake was stronger (r_g = 0.65) than that between backfat thickness and feed intake (r_g = 0.37), which makes it plausible that there is a small negative genetic correlation between stayability of sows and feed intake of finishers. In summary, the association between feed intake and backfat loss during lactation with sow stayability needs further research.

From the genetic correlations, one could arrive at the conclusion that the genetically heavier sows are the most promising. (Genetically) high ad libitum feed intake will yield easy-to-manage sows (less mobilization of body tissue, greater litter weight gain) but has some major disadvantages in lower stayability and lower lactation efficiency. Our study suggests that it is not necessary to increase the feed intake capacity of sows in the short term, because ad libitum feed intake is genetically uncorrelated with traits in a modern breeding goal for dam lines. Lactation efficiency will benefit from a decreased feed intake (capacity).

Simulations

Simulations were performed 1) to evaluate current selection strategies in dam lines, 2) to evaluate the usefulness of lactation efficiency in a breeding goal, and 3) to test the robustness of our results. Performing these simulations gives a better understanding of the biological mechanism of energy metabolism of lactating sows.

Modern Breeding Goal

We simulated a breeding program that yields a balanced genetic progress: improvement of 3 economically important traits. As a consequence, the number of piglets weaned per sow per year will increase. Selection on an index with the total number born, litter mortality, and percent prolonged interval yielded increased stayability as measured by a first-litter survival of sows of 0.6% per generation as a correlated response. Whether this is a biological or managerial phenomenon is unclear. Perhaps sows with a high index, and thus high productivity, were less likely to be culled, which might explain the genetic correlation estimates.

A breeding goal for dam lines with emphasis on the total number born, litter mortality, and percent prolonged interval from weaning to estrus will not dramatically change BW and composition at the beginning of lactation, mobilization of body tissue, and feed intake during lactation. On the other hand, it demonstrates the risks of a modern breeding goal: increased mobilization of body tissue, because feed intake capacity does not keep pace with the increased litter weight gain. Genetic improvement of the total number born, litter mortality, and

percent prolonged interval from weaning to estrus is not a risk for stayability of sows, because the correlated response on stayability was positive.

Given the phenotypic results from Table 3.1, litter mortality decreased from 11.7 to 11.5% after one generation of selection when applying the balanced breeding goal. The total number born increased from 12.56 to 12.75. With an (assumed) farrowing survival of 93%, the number of live born piglets increased from 11.68 to 11.86 piglets per litter. Live born piglets minus mortality yielded 10.31 piglets weaned before and 10.45 piglets weaned after one generation of selection. Lower litter mortality could not prevent the fact that more piglets died during lactation (11.68 −10.31 = 1.37 vs. 11.86 − 10.45 = 1.41). Litter weight at birth increased in such a way that average birth weight also tended to increase. The average birth weight of the base population was 1.369 kg (17.2 kg/12.56 piglets). After one generation of selection, the average individual birth weight became 1.373 kg (17.5/12.75). These are rather small increases; nevertheless, most of the research done in this area has indicated that the average birth weight decreases as a consequence of selection for the total number of piglets born (Kerr and Cameron, 1996; Knol, 2001). Litter weight gain increased, and number of weaned piglets increased as well. However, as a result of selection the average weaning weight decreased by 20 g/weaned piglet per generation [(62.3 + 17.2)/10.31 = 7.71 kg vs. (62.9 + 17.5)/10.45 = 7.69 kg]. A decrease of 20 g per generation is rather small (less than 0.3% of the mean).

As a consequence of selection for reproductive traits (the balanced breeding goal), the fat mass as well as the protein mass of sows decreased, which is favorable for the available energy for production (input) because less energy is needed for maintenance. The correlated response for input is indeed positive. Litter weight gain (and thus output) increased, as did litter weight at birth. When output increases and feed intake does not, the mobilization of body tissue during lactation should increase. Output increased by 0.4 MJ/d per generation. There was a difference in genetic progress between ad libitum feed intake (−0.1 kg/lactation per generation) and restricted feed intake (+0.8 kg/lactation per generation). Nevertheless, mobilization of body tissue increased slightly. Perhaps the emphasis on the interval from weaning to estrus in the breeding goal captured the possible negative consequences of increased mobilization of body tissue, associated with the interval from weaning to estrus. Ad libitum feed intake was genetically uncorrelated with traits in a modern breeding goal for dam lines.

Breeding Goal with Lactation Efficiency Included
Inclusion of lactation efficiency as a selection criterion in a breeding program, with our arbitrary economic weight, was particularly beneficial for the stayability of

sows and (of course) for lactation efficiency itself. Both traits are economically relevant. On the other hand, the negative energy balance during lactation became more severe because mobilization of body tissue increased as a consequence of decreased feed intake (ad libitum and restricted).

Reduced appetite as a consequence of selection on feed efficiency has frequently been reported in finishing pigs (Kanis, 1990; Kerr and Cameron, 1996). Nguyen et al. (2005), on the other hand, reported a negative genetic correlation between residual feed intake and feed intake during a performance test in 2 selection lines; 1 line was selected for high growth rate and 1 was selected for low growth rate. Two studies that have selected directly on feed efficiency in finishing pigs (Jungst et al., 1981; Webb and King, 1983) have reported insignificant responses to several generations of selection on feed intake. Nevertheless, feed intake tended to decrease. Based on these studies, a decreased feed intake might be expected as a consequence of selection for feed efficiency in lactating sows as well.

Despite these factors, inclusion of lactation efficiency as a selection criterion in a breeding program looks quite promising, with no negative consequences for the traditional traits, reduced costs of feed during lactation, and improved stayability of sows. The costs of the breeding program itself would increase, however, because a very intensive registration protocol is needed.

Breeding Goal with Litter Weight Gain
Genetic selection for milk yield in dairy cattle increased feed intake but also resulted in a larger negative energy balance and more mobilization of body tissue during lactation. The magnitude and duration of the negative energy balance are generally related to reduced health and fertility (Veerkamp et al., 2001), and thus probably also to reduced stayability. The simulated selection for litter weight gain only demonstrated the same phenomena in sows. Thus, selection for litter weight gain only yielded increased mobilization of body tissue with decreased stayability. Both other simulations (balanced and balanced with lactation efficiency included) yielded increased mobilization of body tissue with increased stayability. This seems contradictory. Apparently, feed intake plays a key role. In the latter simulations, especially the simulation with lactation efficiency included, feed intake decreased. Genetic selection for litter weight gain only yielded an increased feed intake (ad libitum and restricted).

Future Breeding Goal
All 3 simulations gave the impression of a coherent set of genetic parameters that can be used as a starting point in the development of a breeding program. The

simulation of a balanced breeding goal with or without lactation efficiency demonstrated no risk for the sow in terms of reduced health and fertility. Genetic parameters (and genetic correlations among them) within lines under selection are not constant, but can change in time (Falconer and Mackay, 1996). Conclusions now are not necessarily valid after a number of generations of selection. Although not confirmed in our study, it is expected that increased mobilization of body tissue will eventually cause fertility problems in sows. A lower feed intake capacity will yield increased mobilization of body tissue. A greater feed intake capacity, on the other hand, is a risk for the stayability of the sow. These conclusions plead for keeping the feed intake capacity during lactation more or less constant.

An alternative strategy for genetic improvement of lactation efficiency is to increase the numerator of lactation efficiency (output), rather than reduce the denominator (input). If we succeeded in improving lactation efficiency at an unchanged level of feed intake, it would prevent excessive mobilization of body tissue and would increase the milk production of sows. Increased milk production facilitates sows weaning larger litters. Selection for feed intake in dam lines can serve as an insurance policy for future improvement of sow productivity.

3.5 Implications

The current study yielded a coherent set of genetic parameters that can be used as a starting point for development of a breeding program. A breeding goal for dam lines with emphasis on the total number born, litter mortality, and percent prolonged interval from weaning to estrus will not dramatically change BW and body composition at the beginning of lactation, or mobilization of body tissue and feed intake during lactation. The present levels of performance, expressed as the number of piglets weaned per sow per year, are not a risk for the stayability of sows.

Despite the low heritability, inclusion of lactation efficiency looks quite promising, especially when combined with selection for unchanged feed intake. Such a breeding goal would facilitate future improvement of sow productivity without negative consequences for the sow.

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4

Phenotypic relations between mothering ability, behaviour and feed efficiency of sows peri- and post partum

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Mbstract

A good sow can be characterized by a low piglet mortality and high and uniform piglet weights. To reduce piglet losses and negative effects of increased litter weight gain, mothering ability and feed efficiency are important traits. Behaviour of the sow around and after parturition might be related to mothering ability and feed efficiency during lactation, and behavioural observations can be used as a selection criteria to improve both mothering ability and feed efficiency. The aim of this study was to determine the relationship between behaviour of the sow around and after parturition and the traits litter mortality and feed efficiency during lactation. A total of 78 commercial crossbred sows with parity 1-6 and known litter mortality, genetic merit for mothering ability and feed efficiency during lactation were used in this study. Before parturition sows were individually tested in an open field test and aggression test, where locomotion/position, behaviour and vocalisation were observed during both tests. Around and after parturition position and behaviour of the sow in the farrowing crate were observed, using scan sampling in blocks of five minutes with in total 120 observations per sow. Phenotypic correlation coefficients were calculated between behaviour during tests and in the farrowing crate and litter mortality, genetic merit for mothering ability and feed efficiency during lactation. Results showed that position in the farrowing crate was a good indicator for litter mortality, genetic merit for mothering ability and feed efficiency during lactation. Especially one and two weeks after parturition the sows with lower litter mortality and/or higher genetic merit for mothering ability and feed efficiency during lactation were spending more time lying lateral (P<0.01-0.05), less sitting (P<0.01-0.1) and standing (P<0.05), and they had less postural changes (P<0.01). In the aggression test more vocalising (P<0.05) and less biting (P<0.05) indicated the better sows, whether in the open field test more vocalisation (P<0.05-0.1) and less lying (P<0.05) was observed in the better sows. For the implementation of behavioural observations in selection programs, variance components for behavioural traits have to be estimated and more simple methods to observe large numbers of animals have to be developed.

Key words: Mothering ability, Behaviour, Litter mortality, Lactation efficiency, Sow

4.1 Introduction

Pre weaning mortality among live born piglets (litter mortality) and feed efficiency of sows during lactation are two important traits in sows. Sows are expected to wean large litters, with high and uniform piglet weights. In order to reduce litter mortality, mothering ability is an important trait; it focuses on the influence of the sow on the litter. Besides economically important in itself, improved feed efficiency might help to prevent negative effects of increased litter weight gain until weaning, for example an increased interval weaning to oestrus.

In earlier research, behaviour of the sow around and after parturition appeared to be related to the survival of the piglets. Lying in lateral recumbency, in the farrowing crate or pen, is seen as an optimal position, in order to prevent piglets getting crushed (Jarvis et al., 1999; Marchant et al., 2001; Pedersen et al., 2003). Fewer postural changes are supposed to be advantageous for the pre-weaning survival of the piglets as well (Damm et al., 2005). Fearfulness in sows has been investigated in several studies using behavioural tests. A higher level of fear of humans was found to be correlated with higher litter mortality (Rushen et al., 1999; Janczak et al., 2003). Novelty induced anxiety is often tested in an open field test (Fraser, 1974; Borell and Hurnik, 1991; Taylor and Friend, 1987; Hessing et al., 1994; Fàbrega et al., 2004) and was found to be correlated to higher litter mortality (Janczak et al., 2003), but the results in this study were not significant. Aggressive behaviour in sows towards both humans as piglets was investigated in several studies (Marchant-Forde, 2002; Løvendahl et al., 2005), and a relationship between aggressiveness and behaviour of the sow was found in the study of Ahlstrom et al. (2002) and Andersen et al. (2005).

There might also be a relationship between the behaviour of the sow and feed efficiency during lactation; in a study of McPhee et al. (2001) gilts with a higher lean growth rate on restricted feeding scale spent more time in lateral recumbency and had less postural changes around and after parturition. Bergsma et al. (2009) showed that lactating sows with a higher energetic efficiency had lower mortality among their piglets, piglet growth rate was higher, and at weaning, weights of their piglets were more uniform. They suggested that this phenomenon is (partly) caused by the behaviour of the sow: efficient sows may not use energy in unnecessary activity, reducing the risk of crushing and leaving more energy available for the production of milk. This raises the question: might behaviour of the sow around and after parturition be a mutual explanation for observed differences in litter mortality and feed efficiency during lactation?

Repeatability of litter mortality of 0.05 to 0.07 was found in literature (Hanenberg et al., 2001; Jarvis et al., 2005), but increased for specific causes e.g. crushing (repeatability of 0.14 in Jarvis et al., 2005). Although the heritability of litter mortality was found to be low, ranging from 0.03 to 0.08 (Grandinson et al., 2002; Roehe et al., 2009), selection against mortality during lactation is often practiced in commercial breeding programs. For breeding value estimation, repeated measures (different parities) and family information is used to maximize accuracy. For a more accurate definition of mothering ability the use of a breeding value for mothering ability (besides the phenotypic trait) might be beneficial.

Our basic research question in this study was whether behaviour of the sow around and after parturition was related to phenotypic and genetic differences in litter mortality and to phenotypic differences in feed efficiency during lactation. To find these relationships, we used behavioural tests and observations around parturition. It was hypothesised that sows with lower litter mortality and higher feed efficiency during lactation show low levels of fear and aggressiveness. These sows were predicted to show decreased locomotion and vocalisation and increased explorative behaviour during the open field test, which might indicate a lower level of fear. Additionally, these sows were expected to show less or no aggressive behaviour and more lying lateral in the aggression test, which might reflect calmness and low aggressiveness. In the farrowing crate, these sows were expected to spend more time lying lateral and less time standing, sitting and lying ventral, with less postural changes and activity.

4.2 Material and methods

Animals and housing

The experiment was carried out from April to August 2005, at the experimental farm of the Institute for Pig Genetics in Beilen, The Netherlands. In total, 78 commercial crossbred sows ranging from parity one to six were used in this study. There were three different TOPIGS (pig breeding company TOPIGS, Vught, The Netherlands) crossbreeds present on the farm, two crossbreds were multi-parous sows and one crossbred consisted of only gilts. No hormonal drugs were applied for synchronisation of puberty, oestrus stimulation or to induce farrowing. The experimental farm was under a three week batch farrowing regime; five consecutive farrowing batches were observed.

During gestation, animals were housed in groups of approximately 20 sows. The gestation pens had a partially slatted concrete floor, and provided 2.5 m² of space

per sow. On average, one and a half weeks before farrowing date sows were moved to individual farrowing crates measuring 2.30 m x 1.70 m. Each farrowing room contained eight crates to which sows were allocated at random. The crate was divided into a sow area and a piglet area, the sides of the sow area were provided with bars to prevent the piglets from being crushed when the sow lay down. The floor of the farrowing crate was partly slatted, no substrate was available. During gestation sows were fed 2.5 kg/day (for gilts: 2.2 kg/day) until four weeks before farrowing, and 3.5 kg/day (gilts: 3.2 kg/day) until the sows were moved to the farrowing rooms. Feed was supplied with feeding stations. Sows had 24 h per day access to the feeding station; minimum number of visits was two. When sows were transferred to the farrowing crates, they were gradually adapted to a lactation diet. Sows in the farrowing crates were fed 2.8 kg/day (both sows and gilts), and they were fed twice a day, at 08.00 h and 15.00 h. Three days before expected farrowing sows were fed restricted: 2.5 kg/day for sows and 2.2 kg/day for gilts. After farrowing, the amount of feed raised every day until the sows finally reached the upper limit of 8.0 kg/day at 14 days after farrowing and for the gilts until 6.8 kg/day. Net energy content of the commercial lactation diet, used at the IPG-farm was 9.68 MJ NE per kg. Metabolisable energy was assumed 13.5 MJ ME per kg. The feed supplied contained 147.2 g of crude protein and 8.1 g of lysine per kg diet. Sows had always free access to water from nipple drinkers. In addition to natural light through the window, artificial lights were on between 07.00 h and 15.30 h. Room temperatures in gestation pens varied between 19°C and 21°C and in the farrowing crates around 19°C before farrowing and 25-26°C after farrowing. On extreme warm days, room temperatures were equal to temperature outside.

Open field test

One and a half weeks before parturition, an open field test including novel object was done for each sow individually in random order. Design of the open field test was based on Hessing et al. (1994). Size of the open field was 25 m² (5x5 meter), surrounded by two walls and two solid wooden fences (80 cm high) and a solid concrete floor. Before starting the test, the sow was taken out of the home pen and was brought to the open field by one person. Travelling time from home pen to open field was approximately one minute. The test started as soon as the sow arrived in the open field and lasted 10 minutes. After five minutes, a novel object (bucket with plastic bag) was dropped from the ceiling down onto the floor and then lifted to a height of 30 cm above the floor. Directly after the open field test the sow was transported to the farrowing crate in another building. Faeces and urine were removed from the open field after testing each sow. During the test

locomotion, behaviour and vocalisation were scored, which was a combination of a posture and a behaviour (Table 4.1).

Aggression test

The aggression test was carried out one week before parturition. The sows were in the farrowing crate for already for four days, so they were already adapted to the new environment before the test started. In the test, a small plastic motorised toy pig covered in a furry fabric on batteries (15 cm high, walking and producing a sound) was placed in front of a sow in the farrowing crate for five minutes. The plush pig walked into the direction of the head of the sow. Before starting the test, sows were getting used to the sound of the plush piglet by playing the sound in the farrowing room for one minute to avoid that sows tested first were more afraid of the sound than sows that were tested later. During the test, posture, behaviour and vocalisation of the sow were observed, shown in Table 4.2.

Table 4.1 Ethogram used for the behavioural observations during the open field test..

Behaviour	Definition
Posture	
Walking	locomotion of more than one step
Running	fast locomotion of more than one step
Standing	upright position with four feet on the ground
Kneeling	knees of the forelegs on the ground, feet of hind legs on the ground or in lying position
Sitting	feet of forelegs on the ground, hind legs in lying position
Lying	lying in any position
Behaviour	
Alert	sow is attentive, looking at something
Manipulate novel object	nosing, biting, licking or manipulating novel object
Manipulate floor or wall	nosing, biting, licking or manipulating floor or walls
Touch novel object	touching novel object for the first time
Vocalisation	any vocalisation
Escape	sow tries to escape from the open field
Urinating	sow is urinating
Defecating	sow is defecating
Other	showing no behaviour besides the posture

Table 4.2 Ethogram used for the behavioural observations during the aggression test.

Behaviour	Definition
Posture	
Standing	upright position with four feet on the ground
Kneeling	knees of the forelegs on the ground, feet of hind legs on the ground or in lying position
Sitting	feet of forelegs on the ground, hind legs in lying position
Lying ventrally	one or both forelegs stretched in front of animal
Lying laterally	legs stretched next to animal
Behaviour	
Drinking	drinking of sow
Eating	eating of sow
Defecating	sow is defecating
Urinating	sow is urinating
Alert	sow is attentive, looking at something
Manipulating pen	manipulating pen using nose, mouth or paw
Manipulating floor	manipulating floor using nose, mouth or paw
Manipulate toy	manipulating toy using nose, mouth or paw
Bite toy	sow is biting in toy
Vocalisation	sow is vocalizing
Other	showing no behaviour besides the posture

Behavioural observations around and after parturition

Behavioural observations were carried out for three consecutive days around parturition, for one day on one week after parturition and for one day on two weeks after parturition. Observations were done using scan sampling. The observation days were determined on forehand, depending on the expected farrowing date of the group of sows. As a farm routine, most sows were weaned and inseminated at the same time, and consequently most parturitions were on the three observation days. When parturition appeared to be before of after the three observation days, observations of those particular sows were not included in the analysis. Observations around parturition were carried out from 12.00 till 17.30 h, in blocks of five minutes with in total 50 observations per sow. One and two weeks after parturition observations were done for one day from 09.30 h till 17.30 h, in blocks of five minutes with in total 70 observations per sow. There were no observations around feeding time (15.00 h). During behavioural observations posture and behaviour of the sow were scored, given in Table 4.3.

Based on the behavioural variables, activity and number of postural changes of the sow were calculated. Activity was observed when the sow changed posture and/or switched from behaviour, postural changes only included number of observations

Table 4.3 Ethogram used for the behavioural observations on sows around and after parturition.

Behaviour	Definition
Posture	
Standing	upright position with four feet on the ground
Kneeling	knees of the forelegs on the ground, feet of hind legs on the ground or in lying position
Sitting	feet of forelegs on the ground, hind legs in lying position
Lying ventrally	one or both forelegs stretched in front of animal
Lying laterally	legs stretched next to animal
Behaviour	
Drinking	drinking of sow
Eating	eating of sow
Defecating	sow is defecating
Urinating	sow is urinating
Giving milk	three or more piglets are drinking
Manipulating pen	manipulating pen using nose, mouth or paw
Manipulating floor	manipulating floor using nose, mouth or paw
Head of sow-piglet contact	sow initiated physical contact with head with piglet
Crushing piglet	sow is crushing piglet by lying on the piglet
Biting piglet	sow is biting one of the piglets
Alert	sow is attentive, looking at something
Other	showing no behaviour besides the posture

the sow changed posture. Behavioural traits with a mean percentage below 0.5 were not shown in the tables in the results, but did count for the calculation of postural changes and activity.

Litter mortality and mothering ability

Litter mortality per sow was calculated as the percentage of piglets that died from the total number of piglets to be nursed (exclusive mummies and dead born piglets), averaged over parities. Mothering ability was estimated as a breeding value for each sow (EBV_mothering ability), and was estimated on a weekly basis by breeding company TOPIGS, using a classical animal model:

$$y = Xb + Z_D a_D + Z_F a_F + Wc + e,$$

in which **y** is the vector of observations of individual piglets on survival (0,1 scale); **X**, Z_D, Z_F and **W** are known incidence matrices; **b** is a vector of so-called fixed effects; a_D is a vector of random additive genetic effects (breeding values of the individual piglets), which were assumed to have a normal distribution, $a_D \sim N(0, A\sigma_D^2)$; a_F is a

vector of random genetic foster effects (breeding values of the foster sows which nursed the individual piglets), which were assumed to have a normal distribution, $\mathbf{a_F} \sim N(\mathbf{0}, \mathbf{A}\sigma_F^2)$; $\mathbf{c}$ is a vector of random non-genetic effects common to individuals born in the same litter, with $\mathbf{c} \sim N(\mathbf{0}, \mathbf{I_c}\sigma_c^2)$; and $\mathbf{e}$ is a vector of residuals, with $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I_e}\sigma_e^2)$. For piglet survival from birth until weaning, $\mathbf{b}$ included effects of the gender of the individual (male, female or castrate), the combination of sire line by sow cross of the parents of the animal, the parity of the foster sow (1..6, parity 6 and higher were combined), and the Herd Year Season of birth of the piglets. In addition, $\mathbf{b}$ included a linear regression on birth weight and a linear regression on birth weight variation (defined as STD in birth weight). In pig breeding, it is common practice to adjust survival for birth weight and birth weight variation when known. Common litter effects are routinely included in genetic analyses of pig data, to account for non-genetic covariances between full sibs due to the shared maternal environment.

The breeding value for Mothering ability (EBV_mothering ability) as used in this study refers to the genetic foster effect on survival of piglets from birth until weaning. Mothering ability is expressed as percentage survival of piglets over the lactation. At the time of our study, approximately 1.2 million piglets born on 15 farms in different climate zones and health situations over a period of 12 years were included in the breeding value estimation. An important difference between the traits litter mortality and EBV_mothering ability has to be taken into account, in contrast to the trait litter mortality (higher value means a higher mortality among the piglets) a higher EBV_mothering ability is associated to a lower mortality among the piglets, and subsequently a better performance of the sow.

Feed efficiency during lactation

Feed efficiency during lactation was defined as the energetic efficiency of individual sows during lactation. Definition of energy metabolism of lactating sows was based on on-farm observations of weight and backfat of sows before parturition and at weaning, weight of piglets at birth and at weaning and feed intake of sows during lactation (Bergsma et al., 2009). The feed intake of the sows was observed by the farmer every day. Two feeding schemes were applied, one for primiparous sows and one for multiparous sows. The feeding scheme represented the maximum amount of feed offered to the sow by a feeding device. Once a day the farm manager decided if the amount of feed needed to be down regulated. The decision was based upon the feed intake capacity of the sow, not on the sow's weight, condition or number of piglets to be nursed. Approximately two hours after actual feeding, the sows should have eaten their entire meal; otherwise the feeding

scheme was adjusted. Every time the sow did not eat her entire meal, the feeding scheme was adjusted. Possible refused feed was not weighed back. Feeding higher amounts then the curve happened rarely. The average feed efficiency during lactation at the research farm of IPG is 68%, meaning that 68% of the metabolisable energy through feed intake or mobilization of body tissue above maintenance of the sow (input) was used for piglet growth and piglet maintenance (output). Or as a formula: feed efficiency during lactation (%) = output x 100 / input.

Statistical analysis

The observations in the farrowing pens around and after parturition were all direct observations, done by hand using data sheets. Observations during the open field test and aggression test were done using a Psion Workabout (Noldus Information Technology b.v., Wageningen, The Netherlands). For analysing the observations in the open field test and the aggression test, The Observer version 5.1 software (Noldus Information Technology b.v., Wageningen, The Netherlands) was used. Analysis of all data obtained in this study was done by using the Statistical Analysis System (SAS) version 8.2 (SAS, 1989). Prior to analysis, skewed distribution of litter mortality was transformed: LM transformed = (LM +1) / (number of piglets to wean). Subsequently, litter mortality (transformed) was ranked with Blom score of the RANK procedure in SAS (SAS, 1989).

Pearson correlation coefficients were used in order to investigate the relationships between behaviour and litter mortality, EBV_mothering ability and feed efficiency during lactation. A relation was assumed when the significance of the correlation coefficient was equal to or below P=0.05. There was a small influence of some fixed effects on litter mortality and feed efficiency during lactation (farrowing crate next to corridor yes or no, parity, farrowing compartment, batch number, weight sow after parturition, fat mass sow after parturition, average birth weight live born piglets after cross fostering, and variation birth weight live born piglets after cross fostering), but it did not affect the correlation coefficients (results not shown). Therefore, corrections for fixed effects were not taken into account, and straight forward correlations between behaviour and the traits litter mortality, EBV_mothering ability and feed efficiency during lactation were used.

4.3 Results

Open field test and aggression test

Phenotypic correlation coefficients of behavioural traits in the open field test and aggression test with litter mortality, EBV_mothering ability and feed efficiency during lactation are given in Table 4.4 and 4.5.

The sows with a lower litter mortality showed less lying in the open field after introduction of the novel object (P<0.05), and the more efficient sows vocalised more before introduction of the novel object in the open field test (P<0.05). Vocalisation was also seen more in the sows with lower litter mortality, but the result was not significant (P<0.1). During the aggression test, sows having a higher EBV_mothering ability were vocalising more (P<0.05), and were less biting the plush piglet (P<0.05).

Scan sampling around parturition

Phenotypic correlations between behavioural traits observed around parturition (3 observation days) and litter mortality, EBV_mothering ability and feed efficiency during lactation are given in Table 4.6.

Table 4.4 Open field test: phenotypic correlation coefficients between behavioural traits and litter mortality (LMO), EBV_mothering ability (EBV_{MA}) and lactation efficiency (LE).

Behaviour	Mean	SD	LMO (transformed)	EBV_{MA}	LE
			N = 64	N = 63	N = 58
Before novel object					
Walking (% of total time)	24.4	7.3	-0.10	0.21	0.09
Lying (% of total time)	2.0	7.5	0.02	-0.14	-0.11
Manipulating floor/wall (% of total time)	28.3	18.0	-0.07	0.25†	-0.07
Standing (% of total time)	72.4	10.8	0.09	0.03	0.11
No. of urinating/defecating	1.8	1.4	-0.03	0.03	-0.20
No. of vocalising	2.2	4.9	-0.23†	0.03	0.30*
Alert (% of total time)	2.3	4.7	-0.12	-0.05	-0.05
After novel object					
Walking (% of total time)	14.7	9.2	-0.09	0.17	0.16
Lying (% of total time)	11.2	22.9	0.25*	-0.09	-0.18
Manipulating floor/wall (% of total time)	27.3	16.9	-0.16	0.21†	0.00
Standing (% of total time)	69.7	23.0	-0.11	0.12	0.10
No. of urinating/defecating	0.9	0.8	-0.03	0.14	0.03
No. of vocalising	7.8	17.2	-0.01	0.09	0.13
Alert (% of total time)	10.2	8.0	-0.03	-0.05	-0.08

† P<0.1; * P<0.05; ** P<0.01

Table 4.5 Aggression test: phenotypic correlation coefficients of behavioural traits with litter mortality (LMO), EBV_mothering ability (EBV_{MA}) and lactation efficiency (LE).

Behaviour	Mean	SD	LMO (transformed)	EBV_{MA}	LE
			N = 59	N = 59	N = 53
No. of manipulating floor	0.8	1.5	-0.10	-0.13	0.06
Manipulating floor (%)	0.6	1.3	-0.09	-0.14	0.04
Drinking (%)	0.8	2.8	-0.06	0.12	0.03
Eating (%)	4.5	13.5	0.23†	0.01	0.13
Kneeling (%)	4.5	10.6	-0.16	-0.17	0.07
Sitting (%)	18.0	23.3	0.03	0.07	-0.27†
Standing (%)	33.9	32.6	0.14	-0.09	0.02
Nose-piglet (%)	6.2	11.0	-0.14	-0.05	0.10
No. of nose-big	2.7	3.8	-0.12	-0.12	0.01
Lying lateral (%)	14.1	27.0	0.04	0.22†	0.10
Lying ventral (%)	29.5	30.6	-0.15	-0.09	0.08
Alert (%)	14.8	12.2	-0.11	0.00	-0.21
No. of alert	6.8	4.5	-0.11	-0.13	-0.15
Biting pig (%)	1.6	5.5	0.18	**-0.31***	-0.06
No. of biting pig	0.7	1.9	0.20	-0.16	0.10
Manipulating crate (%)	0.6	2.2	0.03	0.06	-0.13
No. of manipulating crate	0.5	1.2	0.01	0.07	-0.12
No. of vocalisations	32.0	38.3	-0.15	**0.31***	0.16

† P<0.1; * P<0.05; ** P<0.01

Before parturition, no significant correlations were found between behaviour and litter mortality, EBV_mothering ability or feed efficiency during lactation. Shortly after parturition, the high efficient sows were less standing (P<0.05), and had less contact with piglets (P<0.05). Additionally, there was a tendency that the sows with lower litter mortality and higher EBV_mothering ability had fewer postural changes and less activity, but results were not significant (P<0.1).

Scan sampling after parturition
After parturition observations were done for 2 days, at 1 and at 2 weeks after parturition. Behavioural traits showing a significant (P<0.05) positive correlation between the 2 observation days were treated as one trait (mean). Otherwise both observation days were used in the analyses. Phenotypic correlations between behavioural traits observed after parturition (1 and 2 weeks after parturition) and litter mortality, EBV_mothering ability and feed efficiency during lactation are given in Table 4.7.

Table 4.6 Phenotypic correlation coefficients of behavioural traits around parturition (3 observation days) with litter mortality (LMO), EBV_mothering ability (EBV_{MA}) and lactation efficiency (LE).

Behaviour	Mean	SD	LMO (transformed)	EBV_{MA}	LE
Before parturition			N = 40	N = 40	N = 35
Lying lateral	55.2	19.6	-0.07	0.06	0.17
Lying ventral	26.7	15.5	-0.01	-0.03	-0.07
Standing	13.8	10.4	0.17	-0.05	-0.21
Kneeling	0.5	0.9	-0.02	-0.03	-0.12
Sitting	3.9	4.1	-0.06	-0.02	-0.00
Manipulating crate	1.4	3.0	0.19	-0.30†	-0.05
Eating	3.9	4.7	0.12	0.19	-0.15
Drinking	3.1	5.0	0.02	0.16	-0.02
Alert	2.0	3.2	-0.09	-0.11	-0.10
Other (no behaviour)	89.0	8.4	-0.12	-0.04	0.16
Change of posture	18.7	9.9	-0.00	-0.08	-0.33†
Activity	33.8	13.9	0.05	-0.05	-0.33†
After parturition			N = 54	N = 53	N = 50
Lying lateral	72.6	14.9	-0.18	0.21	0.22
Lying ventral	18.6	12.0	0.16	-0.20	-0.11
Standing	6.6	4.7	0.06	-0.12	**-0.31***
Sitting	1.9	2.2	0.25†	-0.10	-0.19
Manipulating crate	0.5	1.2	-0.13	0.10	-0.17
Eating	2.3	2.6	-0.02	-0.20	-0.20
Drinking	1.3	1.7	0.25†	-0.25†	0.03
Contact with piglet	1.9	1.9	-0.17	0.14	**-0.32***
Nursing piglets	38.4	18.2	-0.25†	0.08	0.19
Alert	1.1	1.7	0.01	0.06	-0.02
Other (no behaviour)	54.6	16.4	0.26†	-0.06	-0.14
Change of posture	9.9	6.0	0.24†	-0.24†	-0.26†
Activity	44.8	7.0	0.11	-0.24†	-0.26†

† P<0.1; * P<0.05; ** P<0.01

Sows with a lower litter mortality showed more nursing of piglets after parturition (1 and 2 weeks after parturition) (P<0.05), and less showing no behaviour (P<0.05). Sows with a high EBV_mothering ability were spending more time lying lateral (P<0.05), less sitting (P<0.01) and had fewer postural changes (P<0.01), with all correlations being significant for both 1 and 2 weeks after parturition. Similar behaviour was seen in the high efficient sows during lactation: more lying lateral (P<0.01, less standing (P<0.05), fewer postural changes (P<0.01) and less drinking (all 1 and 2 weeks after parturition) (P<0.05).

Table 4.7 Phenotypic correlation coefficients of behavioural traits during lactation (1 and 2 weeks after parturition) with litter mortality (LMO), EBV_mothering ability (EBV_{MA}) and lactation efficiency (LE).

Behaviour	Mean	SD	LMO (transformed)	EBV_{MA}	LE
			N = 76	N = 75	N = 70
Lying lateral (mean)	111.9	36.0	-0.08	**0.27***	**0.33****
Lying ventral (mean)	56.3	26.2	0.10	-0.22†	-0.19
Standing (mean)	23.6	12.8	0.08	-0.12	**-0.27***
Sitting (mean)	5.8	5.7	0.12	**-0.33****	-0.23†
Nursing (mean)	59.8	18.3	**-0.29***	0.16	0.18
Alert (mean)	2.7	4.6	0.11	0.08	-0.05
Contact with piglet (mean)	4.3	4.3	0.10	0.05	0.12
Drinking (mean)	3.7	3.7	0.09	-0.07	**-0.27***
Changing of posture (mean)	32.7	15.1	0.13	**-0.32****	**-0.38****
Activity (mean)	104.7	15.0	0.06	-0.11	-0.11
Eating week 1	4.5	3.6	0.20†	-0.10	-0.01
Eating week 2	6.0	4.9	-0.17	0.04	-0.19
Other (no behaviour) week 1	60.3	10.6	0.13	-0.08	-0.12
Other (no behaviour) week 2	56.3	13.7	**0.29***	-0.08	0.13

† P<0.1; * P<0.05; ** P<0.01

Relationship between behaviour around and after parturition and behaviour during tests

Behavioural traits observed during scan sampling having a significant effect on litter mortality, EBV_mothering ability or feed efficiency during lactation were correlated to the significant traits observed during the aggression test and open field test. Significant correlations between behaviour in the farrowing crate around and after parturition and behaviour during the open field test and aggression test are given in Table 4.8.

Sows with more manipulation of floor/wall in the open field before introduction of the novel object were showing more contact with piglets (P<0.05), less activity shortly after parturition (P<0.05), and were tending to have less postural changes (P<0.1). After parturition (1 or 2 weeks), these sows were spending less time lying laterally (P<0.05) and more time drinking (P<0.05).

In the aggression test, sows that spent more time in sitting position were also sitting more in the farrowing crate shortly after parturition (P<0.01). Increased biting of the plush piglet was seen in sows that spent more time sitting 1 or 2 weeks after parturition (P<0.05). Sows that were vocalising more in the aggression test appeared to show more lying laterally (P<0.01) and less lying ventrally (P<0.05), were less drinking (P<0.05) and had fewer postural changes (P<0.01).

Table 4.8 Significant correlations between behaviour around and after parturition and the open field test and aggression test. NO = novel object.

Open field test		Aggression test			
Behaviour	*Manipulate floor/wall before NO*	*Sitting*	*Lying*	*Biting*	*Vocalising*
Peri partum	-	-	-	-	-
Manipulate crate	-	-	-	-	-
Postural changes	-	-	-	-	-
Activity	-	-	-	-	-
Post partum	-	-	-	-	-
Sitting	-	**0.41****	-	-	-
Drinking	-	-	-	-	-
Contact piglet	**0.32***	-	-0.26†	-	-
Nursing piglets	-	-	-	-	-
No behaviour	-	-	-	-	-
Postural changes	-0.25†	-	-	-	-
Activity	**-0.36***	-	-	-	-
1-2 weeks post partum	-	-	-	-	-
Lying lateral	**-0.27***	-	-	-	**0.35****
Lying ventral	0.24†	-	-	-	**-0.27***
Standing	0.21†	-	-	-	-0.24†
Sitting	-	-	-	**0.29***	-0.24†
Nursing piglets	-	-	-	-	-
Drinking	**0.25***	-	-	-	**-0.28***
Eating	-	-	-	-	-
Postural changes	-	-	-	-	**-0.34****

† $P<0.1$; * $P<0.05$; ** $P<0.01$

4.4 Discussion

Open field test

Fear in sows is recognized as a negative influence on the performance. A higher level of fear in sows might result in savaging and subsequently in more piglet losses, already mentioned by Marchant-Forde (2002). In several studies, a higher level of fear for humans was observed in an approach test and appeared to be related to higher litter mortality (Rushen et al., 1999; Janczak et al., 2003). Fear may cause more stress in the sow and might therefore be related to higher energy losses and consequently a lower efficiency. Increased walking and vocalising in the open field was supposed to indicate a higher excitement level in the sow (Fraser, 1974; Taylor and Friend, 1987), and subsequently a higher level of fear. More explorative behaviour in the open field was expected to be related to a lower level

of fear, also found by Thodberg et al. (1999). From the results in our study, sows with lower litter mortality and/or a higher breeding value for mothering ability seemed to be less fearful in the open field test, as they were more active and showed more explorative behaviour, where the latter was related to more manipulation of the wall or floor in the open field. On the other hand, these sows showed increased vocalisation in the open field before introducing the novel object, which would indicate more fear according to Thodberg et al. (1999). However, as the increased vocalisation only occurred before introduction of the novel object, it can also indicate that these sows are more alert during the test, and maybe also more alert (and therefore more careful) later towards their piglets. To get more insight in the relationship between vocalisation and mothering ability, it would be interesting to include the type of vocalisation, which was not taking into account in the current study.

It may be questioned whether the open field test in this study was a good test to identify fearful behaviour in the sows. Sows were calm when entering the open field and reaction of the sows on the novel object was less strong then expected; possibly no fearful behaviour was present in part of the sows. Some sows continued their behaviour when the novel object (bucket) was coming down and seemed not to be disturbed. Experiences earlier in life may have a large influence on the way a sow deals with a stressful or fearful situation, and older sows may be relatively more adapted to such situations resulting in less fear, also mentioned by Janczak et al. (2003). Furthermore, the way a sow responds to and deals with stress or fear in the open field may differ between animals. The existence of different coping styles in pigs and the influence on their behaviour were mentioned in several studies (Hessing et al., 1994; Ruis et al., 2000; Erp-van der Kooij et al., 2002; Bolhuis, 2004), and may explain the differences in behaviour in the open field. A sow in a fearful situation can show increased locomotion in order to avoid the stressor, but also immobility (freeze). In order to interpret behaviour in the open field correctly, coping style or 'personality' of the sow might have to be taken into account.

Aggression test

To investigate the response of a sow towards piglets, different tests have been developed in various studies. In a study of Grandinson et al. (2003) the piglet scream test was used to observe the reaction of a sow to the distress call from a piglet, as when it is being crushed under the sow. A strong reaction to the distress call was associated with low mortality in the litter. Aggressiveness towards a strange female pig was investigated by Janczak et al. (2003) using a resident-

intruder test, but the relation between aggressiveness and the performance of the sow later in life was not investigated. Fear and/or aggression of a sow towards humans were tested in several studies using a human approach test (Marchant-Forde, 2002; Janczak et al., 2003; Grandinson et al., 2003). However, in the study of Marchant-Forde (2002) no relation was found between aggressiveness towards a stockperson and savaging piglets. Fearful and aggressive behaviour towards humans in a human approach test might be completely different from the behaviour towards piglets and litter mortality. It has been hypothesised among farmers that sows which are highly aggressive towards humans are better mothers, but such relationships were never found (Grandinson et al., 2003).

In order to observe the direct fear and aggression of a sow towards her piglets, an aggression test with a plush piglet was developed in this study. In the sows with higher EBV_mothering ability we saw more vocalisation and less biting the plush piglet. These results might indicate that these sows were more responding to the plush piglet, and with more care and less aggression than the sows with lower mothering ability. However, the correlations between mothering ability and these to behavioural traits were only moderate, and no other significant correlations were found in this test, so this aggression test might not be very suitable as a way to identify better sows. Furthermore, we do not know if the sow perceive the plush toy as a real piglet, and therefore the behaviour of the sow towards the plush piglet may not completely be related to their behaviour towards a real piglet. Nevertheless, this test might give more insight in the behaviour of sows in relation to mothering ability.

Scan sampling around and after parturition

The position of the sow in the farrowing crate has an important influence on litter mortality, one of the common causes of piglet mortality is overlying by the sow (Vieuille et al., 2003; Valros et al., 2003; Andersen et al., 2005). Optimal position of a sow is in lateral recumbency with few postural changes, in that way piglets have an optimal access to the udder and have less chance of being crushed (Marchant et al., 2001; Pedersen et al., 2003). In the current study, we hardly found any significant correlation between mothering ability, litter mortality and efficiency during lactation and position in the farrowing crate around parturition, but we did find several significant correlations 1 or 2 weeks after parturition. Results were in agreement with the formulated hypothesis; sows with a higher merit for mothering ability were spending more time lying laterally and sows with lower litter mortality were spending more time nursing piglets shortly after parturition. Lying in lateral position was also seen more in sows with a higher feed efficiency during lactation,

which was already suggested by Bergsma et al. (2009). These sows may spill less energy by spending more time lying laterally and they are able to use this energy for a higher milk production. Additionally, spending more time in lateral recumbency may indicate a reduced stress level in these sows, resulting in less energy losses due to reduced stress related behaviour.

The posture sitting was seen more in the sows with higher litter mortality and lower EBV_mothering ability. This posture may indicate that the sow is trying to avoid stimulation of the udder by the piglets, which might have a negative influence on the growth and survival of the piglets. A longer time spending in sitting position might also be a reflection of a higher level of fear or stress. Some sows changed from a lying to a sitting position during the observations, as a reaction on the presence of the researcher in the farrowing room. The sows with a lower feed efficiency during lactation were also spending more time standing, this might indicate a higher level of stress with more energy that is used, and therefore the feed efficiency of the sow will decrease. Besides sitting, we also saw more postural changes in the sows with lower EBV_mothering ability. Postural changes of the sow in the farrowing crate are recognized as risky movements, since crushing by the sow is one of the predominant causes of piglet mortality (Damm et al., 2005). In the study of Marchant et al. (2001), crushing by the sow accounted for 75% of the liveborn piglet deaths. A high number of postural changes related to higher litter mortality was also found in the study of Marchant (2001). More postural changes after parturition was also seen in the less efficient sows during lactation. More postural changes made by the sow results in less energy left for the piglets, and therefore a lower feed efficiency. Comparable results were seen in a study with White Leghorns selected for high and low feed efficiency, where activity of the animals was negatively correlated with feed efficiency (Luiting et al., 1991).

A contrary relation between activity of the sow and litter mortality was seen in a study of Valros et al. (2003), where sows with a higher activity level had a low number of piglets died. According to Valros et al. (2003) sows with a higher activity level in the farrowing pen have a higher response to piglet stimuli, which is beneficial for the piglets. However, activity level in this study was calculated as the percentage of the observations a sow was standing or walking. Calculation of activity was based on the number of times a sow changes her position and/or behaviour between two observations. In the study of Valros et al. (2003) no correlation was found between frequency of standing-to-lying events and litter mortality. In addition, sows were kept in pens where more space is available for gross body movements. It is known that behaviour of sows in farrowing pens is quite different from the behaviour in crates (Blackshaw et al., 1994; Thodberg et

al., 2002; Damm et al., 2005), in pens sows have to be more careful for piglets not getting crushed compared to crates. Therefore, the behaviour we would like to see in sows housed in crates might be different from the preferred behaviour of sows in pens with more space available.

Overestimation of significant correlations between behaviour in the farrowing crate and performance of the sow might have happened due to auto correlation. When a high percentage lying laterally was found, consequently the percentage standing or sitting is low. In that way, a high significant correlation with one postural trait means often also a high significant correlation with the other postural traits. Furthermore, some behavioural traits were automatically connected to a certain posture, like drinking and standing or lying lateral and nursing piglets. In that way, some traits might show a significant effect, but only because these traits are related to an other highly significant trait. Besides this problem of autocorrelation, we also have to be cautious about the interpreting of the results, as some significant correlations might occur by chance due to the many correlations used.

Relationship between behaviour around and after parturition and behaviour during tests

Manipulation of floor or wall in the open field test was seen as a favourable trait, and was also correlated to less activity, which was seen in the better sows. However, more manipulation of floor or wall in the open field was related to less lying lateral in the farrowing crate after parturition, which was seen in the sows with higher litter mortality and lower feed efficiency during lactation. As already mentioned earlier, it is difficult to interpret behaviour in the open field test correctly, and therefore the test might not be suitable for recognizing the better sows.

More vocalisation in the aggression test was related to more lying lateral and less lying ventral, and also less postural changes in the farrowing crate one or two weeks after parturition. These behavioural traits observed in the farrowing crate were all related to lower litter mortality and a higher feed efficiency during lactation, therefore vocalisation during the aggression test seems to be a very good indicator for a better performance of the sow. More vocalisation in the aggression test might indicate more responsiveness to the plush piglet and also more care to their own piglets. Attentiveness to piglets can be interpreted as a positive behavioural trait, in the study of Grandinson et al. (2003) better sows (with lower litter mortality) were showing a strong reaction to distress calls of a piglet. The posture sitting in the farrowing crate around and after parturition might also be a

good indicator for the performance of the sow, as it was positively correlated to sitting in the aggression test and being aggressive towards the plush piglet.

In conclusion, behavioural observations after parturition using scan sampling appeared to be a good method to recognize the behaviour of sows with high mothering ability and a high feed efficiency during lactation. Especially posture and postural changes in the farrowing crate are good indicators for mothering ability and feed efficiency during lactation, and can be used to further improve the performance of sows. The open field test and aggression test are good ways to get more insight in the behaviour of the sow, but they are less suitable to predict the better sows according to the low number of significant results, and both tests are very time consuming to apply in practise. In the future, research has to be focussed on the development of simple methods to observe large numbers of animals, and variance components for behavioural traits have to be estimated to find out whether selection of sows based on behavioural observations is possible.

Acknowledgements

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5

The contribution of social effects to heritable variation in finishing traits of domestic pigs (Sus scrofa)

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Abstract

Social interactions among individuals are ubiquitous both in animals and plants, and in natural as well as domestic populations. These interactions affect both the direction and magnitude of responses to selection, and are a key factor in evolutionary success of species and in the design of breeding schemes in agriculture. At present, however, very little is known of the contribution of social effects to heritable variance in trait values. Here we present estimates of the direct and social genetic variance in growth rate, feed intake, back fat thickness and muscle depth in a population of 14,032 domestic pigs with known pedigree. Results show that social effects contribute the vast majority of heritable variance in growth rate and feed intake in this population. Total heritable variance expressed relative to phenotypic variance equaled 71% for growth rate and 70% for feed intake. These values clearly exceed the usual range of heritability for those traits. Back fat thickness and muscle depth showed no heritable variance due to social effects. Our results suggest that genetic improvement in agriculture can be substantially advanced by redirecting breeding schemes, so as to capture heritable variance due to social effects.

Key words: Quantitative genetics; Multilevel selection, Pigs, Social interactions, Indirect genetic effects

5.1 Introduction

Social interactions among individuals are ubiquitous both in animals and plants, and in natural as well as domestic populations. These interactions affect both the direction and magnitude of responses to artificial and natural selection (e.g. Wilham, 1963; Hamilton, 1964; Griffing, 1967; Wade, 1977; Frank, 1998; Wolf et al., 1998). Social interactions, therefore, are a key factor in the design of artificial breeding programs in domestic species (Denison et al., 2003; Muir, 2005), and for the outcome of evolutionary processes in natural populations (e.g. Hamilton, 1964; Queller, 1992; Frank, 1998; Keller, 1999; Clutton-brock, 2002).

In agriculture, reduction of competitive behaviors is critical for improving animal well-being and productivity in confined high-intensity rearing conditions (Craig and Muir, 1996; Kestemont et al., 2003; MUIR 2005). Both theoretical and empirical work has shown that the relatedness among interacting individuals and the distribution of selection pressure over the individual and group level are key factors for response to selection (Griffing, 1967, 1976; Muir, 1996; Craig and Muir 1996; Bijma et al., 2007a). In evolutionary biology, the debate centers on the evolution of social behaviors such as altruism and cooperation, and whether those can be explained by interactions among relatives and selection acting at multiple levels (Hamilton, 1964; Michod 1982; Wade 1978, 1985; Frank, 1998; Wolf et al. 1998; Keller 1999).

In evolutionary biology, numerous theoretical models have been proposed for understanding the consequences of social interactions, and seemingly different models often appear to be equivalent formulations of the same process (Keller 1999; Lehmann and Keller, 2006; Lehmann et al., 2007). There is an urgent need, however, for modeling approaches that can be applied empirically, so as to bring theory and observation into closer contact (Leimar and Hammerstein, 2006, Lehmann et al., 2007). Quantitative genetics has a strong tradition of combining theory and application (Falconer and Mackay 1996; Lynch and Walsh, 1998). In particular the so-called animal model, combined with maximum likelihood methodology, has proven to be a powerful and flexible tool for genetic analysis of complex traits in real populations (Patterson and Thompson, 1971; Henderson, 1975; Sorenson and Kennedy, 1986; Lynch and Walsh, 1998 and references therein; Kruuk 2004).

Muir and Schinkel (2002) extended the animal model to analyze socially affected traits. Subsequent work, however, suggested that genetic parameters of social effects are difficult to estimate (Van Vleck and Cassaday 2005; Arango et al., 2005;

Van Vleck et al., 2007). Those studies presented results from different statistical models, often with non-significant and unexpected results, and did not clarify the implications of observed results for genetic theory and response to selection. As a consequence, the magnitude of heritable social effects and its consequences for response to selection are still largely unclear.

Recently, Muir (2005) and Bijma et al. (2007a,b) presented a quantitative genetic framework for the prediction of response to selection, and for statistical analyses of traits affected by social interactions. Together with the work of Ellen et al. (2007), this work combines classical and socially affected traits into a single quantitative genetic framework. By adding a level of individual-by-individual interaction to the classical variance components, Bijma et al. (2007a) showed that social interactions among individuals generate an additional level of heritable variation. This additional heritable variation is not part of the observed phenotypic variance, meaning that socially affected traits may posses a heritable variance exceeding observed phenotypic variance. As a consequence, response of socially affected traits to selection can be very large compared to observed variability among individuals, at least in theory. Bijma et al. (2007b) show that the quantitative genetic model for socially affected traits dictates which components to include in statistical models for analyzing real data, in particular for the non-heritable component of social effects. Application to mortality due to cannibalistic behavior in domestic chicken showed that heritable variance in mortality was two- to three-fold greater than classical additive genetic variance (Bijma et al., 2007b; Ellen et al., 2008).

At present, still very little is known of the genetic parameters underlying socially affected traits. Here we present estimated genetic parameters for direct and social genetic effects on growth rate, feed intake, back fat thickness and muscle depth in domestic pigs (Sus scrofa). Our results will show that social effects contribute the vast majority of heritable variance in growth rate and feed intake in this population.

5.2 Theory

This section summarizes the quantitative genetic theory for traits affected by social interactions presented in Bijma et al. (2007a), emphasizing the consequences for heritable variance. In classical quantitative genetics, observed trait values (P) are the sum of a heritable component (A, breeding value), and a non-heritable component (E, environment); $P = A + E$ (Falconer and Mackay, 1996; Lynch and Walsh, 1998). When trait values of individuals are affected by interactions with

others, this model needs to be expanded with social effects (Dickerson, 1947; Wilham, 1963; Griffing, 1967; Cheverud, 1984; Wolf et al., 1998). When interactions take place within groups of n individuals, the trait value of each individual may be modeled as the sum of a direct effect rooted in the individual itself, and the summed social effects due its $n-1$ group members. Both direct and social effects may be decomposed into a heritable component, *A*, and a non-heritable component, *E*, so that the trait value of individual *i* is

$$P_i = A_{D,i} + E_{D,i} + \sum_{i \neq j}^{n-1}(A_{S,j} + E_{S,j}) \tag{1}$$

(Griffing, 1967), in which $A_{D,i}$ is the heritable direct effect of individual *i* on its own trait value, $E_{D,i}$ is the corresponding non-heritable direct effect, $A_{S,j}$ is the heritable social effect of group member *j* on the trait value of *i*, $E_{S,j}$ is the corresponding non-heritable social effect, and $\sum_{i \neq j}^{n-1}$ represents the sum taken over the $n-1$ group members of *i*. Henceforth, we will refer to A_D and A_S as direct and social breeding values (DBV and SBV). It follows from Equation 1 that the phenotypic variance equals

$$\sigma_P^2 = \sigma_{A_D}^2 + \sigma_{E_D}^2 + (n-1)\left(\sigma_{A_S}^2 + \sigma_{E_S}^2\right) + (n-1)r\left[2\sigma_{A_{DS}} + (n-2)\sigma_{A_S}^2\right] \tag{2}$$

(Arango et al., 2005; See appendix for derivation), in which σ^2 denotes variance, $\sigma_{A_{DS}}$ the covariance between direct and social breeding values of individuals, and *r* mean additive genetic relatedness among group members (The *r* is twice the mean pair-wise coefficient of coancestry between group members; Lynch and Walsh, 1998).

Because each individual interacts with $n-1$ others, the total heritable impact of an individual on the mean trait value of the population is the sum of the individual's DBV and $n-1$ times its SBV. Bijma et al. (2007a), therefore, defined the Total Breeding Value,

$$TBV_i = A_{D,i} + (n-1)A_{S,i}. \tag{3}$$

The TBV is a generalization of the usual breeding value, to account for heritable social effects on trait values. Analogous to classical theory, response to selection equals the change in mean TBV per generation, $\Delta\overline{P} = \Delta\overline{TBV} = \Delta\overline{A}_D + (n-1)\Delta\overline{A}_S$. The $\Delta\overline{A}_D$ represents the usual response to selection, whereas the

$(n-1)\Delta\overline{A}_S$ represents the response originating from the change in mean social environment that individuals experience.

In classical theory, heritable variance in trait value is the variance of breeding values among individuals. Analogously, for socially affected traits, heritable variance is the variance of TBV's among individuals (Bijma et al., 2007a),

$$\sigma^2_{TBV} = \sigma^2_{A_D} + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma^2_{A_S}. \tag{4}$$

In Equation 4, $\sigma^2_{A_D}$ represents the usual additive genetic variance, whereas the $2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma^2_{A_S}$ represents the additional heritable variance due to social effects. Equation 4 shows that heritable social effects may substantially increase heritable variance, in particular with large groups. (Although σ^2_{TBV} may be smaller than $\sigma^2_{A_D}$ when $\sigma_{A_{DS}}$ is strongly negative). Increased heritable variance translates directly into increased potential for response to selection. Ellen et al. (2007) show that response to selection equals $\Delta\overline{P} = \iota\rho\sigma_{TBV}$, in which ι represents the intensity of selection, and ρ the correlation between the selection criterion and the TBV of individuals. This expression is fully analogous to the classical expression for response, $\Delta\overline{P} = \iota\rho\sigma_A$, in which ρ represents the correlation between the selection criterion and the classical breeding value (Falconer and Mackay, 1996). Thus the σ^2_{TBV} truly represents the potential of a trait to respond to selection.

In classical theory, an individual's breeding value (*A*) is a component of its trait value, $P_i = A_i + E_i$. As a consequence, heritable variance is smaller than phenotypic variance, and heritability is smaller than one. With heritable social effects, however, an individual's TBV is not a component of its trait value; $P_i \neq TBV_i + E_i$. The trait value of an individual contains social components originating from others (Equation 1), whereas the TBV consists entirely of heritable effects originating from the individual itself (Equation 3). Because the TBV is not a component of the trait value, phenotypic variance does not present an upper limit for heritable variance. With socially affected traits, therefore, heritable variance may exceed phenotypic variance. For example, if direct and social effects are independent and of equal magnitude, heritable effects account for half of the phenotypic variance, and groups are composed of four unrelated individuals, then heritable variance is 125% of phenotypic variance. (For example, $\sigma_{A_{DS}} = \sigma_{E_{DS}} = 0$, $\sigma^2_{A_D} = \sigma^2_{E_D} = 1$, $\sigma^2_{A_S} = \sigma^2_{E_S} = 1$, $n = 4$, and $r = 0 \rightarrow \sigma^2_{TBV} = 10$ and $\sigma^2_P = 8$.) This example illustrates that social effects create hidden heritable variance. Part of the heritable variance is hidden, because the TBV of an individual is spread across trait values of n distinct individuals, and does, therefore, not surface in phenotypic variance.

To express heritable variance relative to phenotypic variance, we introduce

$$T^2 = \sigma_{TBV}^2 / \sigma_P^2, \tag{5}$$

which is an analogy of $h^2 = \sigma_A^2 / \sigma_P^2$, although T^2 may exceed one. Note that T^2 is not a true heritability, but represents heritable variance expressed on the scale of phenotypic variance among individuals. Comparison of T^2 and classical $h^2 = \sigma_A^2 / \sigma_P^2$ allows quick judgment of the contribution of social effects to heritable variance. For example, with $h^2 = 0.3$ and $T^2 = 0.6$, total heritable variance is two times greater than classical (direct) additive genetic variance, meaning that social effects contribute 50%. In the following, we describe the estimation of $\sigma_{A_D}^2$, $\sigma_{A_S}^2$, $\sigma_{A_{DS}}$, and σ_{TBV}^2 in a population of domestic pigs.

5.3 Material

Data originated from the experimental farm of the Institute for Pig Genetics, located in Beilen, the Netherlands. This is a farrow-to-finish farm of 170 crossbred sows and a rotational use of six sire lines in a three week system, with direct comparison of alternating combinations of two sire lines at any time. Five sow crosses were used as dams of the finishing pigs; two sow crosses were present at any time. To disentangle the common environment among litter mates due to the biological mother from that due to the foster mother, at least 25% of the live born piglets of each sows were cross-fostered during the weaning period (i.e. before the start of the finishing period).

Data consisted of records on 14,032 finishing pigs, descending from 397 sires and 580 dams. Table 5.1 shows the distribution of observations (animals with slaughter record), number of sires and number of dams over the different combinations of sire lines and sow crosses. Pens consisted of 6 to 12 animals of the same gender (male, female or castrate). The penning strategy aimed at reducing variation in penning weight within pens. Due to the working method on the farm, the probability of penning litter mates together was higher than for penning at random. As a consequence, average relatedness within pen was 0.18, ranging from 0.01 to 0.51. Relatedness was calculated using 3 generations of pedigree.

About one third of the finishing pigs of each cross were fed ad libitum, using IVOG (INSENTEC, Marknesse, The Netherlands) feeding stations to record feed intake (Table 5.2). With ad libitum feeding, average daily eating time was ~1 hr per individual. Because maximum pen size was 12 individuals, feeding stations were

Table 5.1 Number of individuals with observations on slaughter traits, and number of sires and dams for each combination of sire line and dam cross.

Sire line		Sow cross					
		A	B	C	D	E	All
F	Individuals	305	55	310	18	122	810
	Sires	13	7	17	5	10	32
	Dams	31	14	33	7	36	121
G	Individuals	453	341	161	.	.	955
	Sires	30	16	12	.	.	37
	Dams	47	43	20	.	.	110
H	Individuals	1,417	1,001	353	125	1,031	3,927
	Sires	80	50	24	22	41	117
	Dams	121	92	39	17	102	371
I	Individuals	1,042	1,012	583	113	579	3,329
	Sires	61	38	33	18	23	91
	Dams	84	101	52	21	77	335
J	Individuals	924	1,147	222	135	1,024	3,452
	Sires	49	43	15	18	46	97
	Dams	78	101	28	21	102	330
K	Individuals	232	579	261	83	404	1,559
	Sires	14	12	11	9	9	23
	Dams	27	78	34	13	50	202
All	Individuals	4,373	4,135	1,890	474	3,160	14,032
	Sires	247	166	112	72	129	397
	Dams	153	145	88	37	157	580

vacant at least 50% of the day, and thus available for (submissive) animals. The remaining two-third of the finishing pigs was fed restricted at group level during the entire finishing period. Individual feed intake was unknown for restricted fed animals. On pen level, restricted feed intake was ~90% of feed intake in ad libitum fed pens. For restricted fed animals, the amount of feed per pen was transported once a day to the dry feeders, which took ~4 hr for the entire farm and started at 8:00 AM. Per pen, only one animal at a time could use the dry feeder. A nipple drinker was mounted over the feeding pan of the dry feeder.

All finishers were weighed individually at start of the finishing period at ~27 kg. At slaughter, hot carcass weight was recorded along with back fat thickness and muscle depth using the Hennessy Grading Probe. Four traits were analyzed: growth rate (g/d), back fat thickness (mm), muscle depth (mm) and feed intake (g/d). Growth rate was calculated as calculated live weight minus penning weight, divided by the length of the finishing period. Live weight was calculated as $1.3 \times HotCarcassWeight - 0.0025 \times HotCarcassWeight^2 + 0.2075 \times HotCarcassWeight$

(Handboek Varkenshouderij, 2004). Feed intake was calculated as cumulative feed intake during the finishing period, divided by the length of the finishing period. Table 5.2 shows the number of observations and means for all traits. Ad libitum fed animals had higher growth rate and a somewhat higher back fat thickness and muscle depth than restricted fed animals. The number of animals with slaughter records was ~15% lower than the number of penned animals, mainly due to loss of information, such as ear tags.

5.4 Methods

Genetic parameters were estimated using residual maximum likelihood (ReML) with an animal model (Patterson and Thompson, 1971; Henderson, 1975; Lynch and Walsh, 1998; Kruuk, 2004). Three models were compared. First, the classical animal model (Model 1). Second, the classical animal model extended with non-heritable social effects of pen mates (Model 2). Third, the classical animal model extended with both heritable and non-heritable social effects of pen mates (Model 3).

Model 1 was

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{c} + \mathrm{e}, \tag{6}$$

in which $\mathbf{y}$ is the vector of observations; $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are known incidence matrices; $\mathbf{b}$ is a vector of so-called fixed effects, which account for systematic non-genetic

Table 5.2 Number of observations and means of traits per feeding strategy.

	Feeding strategy		All
	Restricted[1]	*Ad libitum*	
No. of animals penned	11,469	4,965	16,434
Penning weight, kg	27.7	27.2	27.6
No. of animals with slaughter records	9,541	4,491	14,032
Hot carcass weight, kg	86.3	88.9	87.1
Growth rate, g/d	823	881	841
Back fat thickness, mm	16.6	17.6	16.9
Muscle depth, mm	57.2	58.6	57.6
No. of animals with individual feed intake	0 [2]	4,342	4,342
Feed intake, g/d	- [2]	2,141	2,141

[1] The amount of feed was restricted per pen.
[2] Individual feed intake of restricted fed animals was unknown.

differences between groups of individuals (see below); **a** is a vector of random additive genetic effects (breeding values), which were assumed to follow a normal distribution, $\mathbf{a} \sim N(\mathbf{0}, A\sigma_A^2)$; **c** is a vector of random non-genetic effects common to individuals born in the same litter, with $\mathbf{c} \sim N(\mathbf{0}, I_c\sigma_c^2)$; and **e** is a vector of residuals, with $\mathbf{e} \sim N(\mathbf{0}, I_e\sigma_e^2)$. The I_c and I_e are identity matrices of the appropriate dimensions, and **A** is a matrix of additive genetic relationships among all individuals (e.g. Lynch and Walsh, 1998). Common litter effects are routinely included in genetic analyses of pig data, to account for non-genetic covariances between full sibs due to the shared maternal environment.

The fixed effects depended on the trait analyzed. For growth rate, **b** included effects of the number of pen mates, the gender of the individual (male, female or castrate), the combination of sire line by sow cross of the parents of the animal (1..28), the feeding strategy (restricted or ad libitum), and the compartment in which the pen was located (1..18). In addition, **b** included a linear regression on hot carcass weight in the analyses of back fat thickness and muscle depth, and a linear regression on body weight at penning in the analysis of feed intake. In pig breeding, it is common practice to adjust back fat thickness and muscle depth for carcass weight, and to adjust feed intake for penning weight when known.

Model 2 accounted for non-heritable social effects ($\sigma_{E_S}^2 > 0$). Non-heritable social effects create a non-genetic covariance among pen mates equal to $Cov_{penmates} = 2\sigma_{E_{DS}} + (n-2)\sigma_{E_S}^2$ (Bijma et al., 2007b). Bijma et al. (2007b) showed that even a small non-genetic covariance among pen mates may substantially bias the estimated genetic parameters, illustrating the need to account for such covariance in the statistical analysis. To account for this covariance, Bijma et al. (2007b) fitted a correlation between residuals of group members, which is the general solution allowing any $Cov_{penmates}$. However, when $Cov_{penmates}$ is positive, which is likely unless n is small, an equivalent but simpler solution is to fit random pen effects rather than correlated residuals within pens. It follows from the general statistical result that 'covariance within groups equals variance among group means', that the variance of the random group effect equals $Var_{groupmeans} = Cov_{penmates} = 2\sigma_{E_{DS}} + (n-2)\sigma_{E_S}^2$. (Our simulated data confirmed equivalence of both models as long as $Cov_{penmates} \geq 0$, results not shown.) Preliminary analyses confirmed that $Cov_{penmates}$ was positive for all traits in our data. We, therefore, fitted a random group effect, which converged easier and took less computing time than fitting correlated residuals. (Note, we use "group" to refer to the animals in the same pen.) Thus Model 2 was

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{c} + \mathbf{V}\mathbf{g} + \mathrm{e}, \tag{7}$$

in which $\mathbf{V}$ is a known incidence matrix for groups and $\mathbf{g}$ a vector of random group effects, with $\mathbf{g} \sim N(\mathbf{0}, \mathbf{I}_g \sigma_g^2)$. Other elements were the same as in Model 1.

Model 3 accounted for both heritable and non-heritable social effects,

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_D \mathbf{a}_D + \mathbf{Z}_S \mathbf{a}_S + \mathbf{W}\mathbf{c} + \mathbf{V}\mathbf{g} + \mathrm{e}, \tag{8}$$

in which $\mathbf{Z}_D$ and $\mathbf{Z}_S$ are known incidence matrices for direct and social genetic effects, and $\mathbf{a}_D$ and $\mathbf{a}_S$ are vectors of random direct and social genetic effects, with

$$\begin{bmatrix} \mathbf{a}_D \\ \mathbf{a}_S \end{bmatrix} \sim MVN \otimes (\mathbf{0}, \mathbf{C} \otimes \mathbf{A}),$$

in which

$$\mathbf{C} = \begin{bmatrix} \sigma_{A_D}^2 & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma_{A_S}^2 \end{bmatrix}$$

and $\otimes$ indicates the Kronecker product of matrices. Other elements were the same as in Model 2. In Model 3, the $\mathbf{Z}_S \mathbf{a}_S$ accounts for heritable social effects, whereas the $\mathbf{V}\mathbf{g}$ accounts for the non-heritable social effects. The $\mathbf{Z}_D$-matrix in Model 3 is identical to the $\mathbf{Z}$-matrix in Models 1 and 2; In model 3, we included the subscript D to emphasize the difference with $\mathbf{Z}_S$.

All models were fitted using ReML as implemented in the ASREML software (Gilmour et al., 2002). Traits were analyzed univariately. Thus four separate analyses were done, one for each trait. All penned animals were included in the analyses, even when their slaughter records were missing. Because maximum group size was 12 animals, the design matrix $\mathbf{Z}_S$ had 11 columns; one for each group member. For groups smaller than 12 animals, $\mathbf{Z}_S$ contained a 1 for each of the n group members, while the remaining $(12 - n)$ elements of $\mathbf{Z}_S$ were set to missing. The matrix of additive genetic relationships, **A**, was calculated using information on three generations of pedigree. A total of 19,674 animals were included in the pedigree. Animals in the pedigree originated from 13 genetic groups, each representing a particular boar or sow line. To account for a possible effect due to genetic groups, groups were accounted for in the calculation of the **A**-matrix (Thompson, 1979).

Validation focused on growth rate. To validate our results, we performed three additional analyses. First, we extensively tested alternative models, so as to identify non-genetic factors confounded with heritable social effects, thus causing false

positive results (see Appendix). Second, we evaluated the predictive ability of estimated classical breeding values vs. estimated direct and social breeding values. For this purpose, the observation on growth rate of every tenth animal was omitted from the data, but the animal remained in the pedigree-file. Next, ASREML was used to estimate either classical breeding values or direct and social breeding values for all animals, including those whose record had been set to missing. Subsequently, values of the records set to missing were predicted using the estimated fixed effects and either the estimated classical breeding values or the estimated direct and social breeding values. Analysis of variance was used to evaluate the predictive ability of the estimated classical breeding values versus the estimated direct and social breeding values (using PROC GLM of SAS). Third, we used independent data on 13,168 individuals of a different population descending from the same genetic lines, collected on a different farm, to obtain an independent estimate of the genetic parameters. These data did not overlap with the data described above, but contained information on growth rate only; independent data on the other traits were not available. Pen size was 10 animals. Data were analyzed using Model 3.

5.5 Results

For all traits, heritabilities from Model 1 were in line with the literature, though the estimate for feed intake was in the upper range (Table 5.3; Cutter and Brascamp, 1998). For growth rate and feed intake, a likelihood ratio test strongly favored Model 2 over Model 1 ($p \ll 0.001$). Results from Model 2 revealed a substantial variance of the pen effect for growth rate and feed intake, whereas estimates for back fat thickness and muscle depth were small (Table 5.4). Pen effects contributed 27% of phenotypic variance in growth rate, and even 42% of phenotypic variance in feed intake. Inclusion of pen effects reduced estimated genetic, common litter and residual variances (Table 5.4 vs. Table 5.3). As a result, heritability dropped from 0.36 to 0.25 for growth rate, and from 0.41 to 0.18 for feed intake. This shift indicates a partial confounding of pen and pedigree, which agrees with the above average relatedness among pen mates (see 5.3 Material). Due to the relatedness among pen mates, covariances among pen mates are fitted as heritable variance when pen effects are omitted from the model.

Accounting for pen effects is not common in pig breeding, because physical differences among pens are usually minor and pen number is often not recorded. Also in our data, physical differences among pens were negligible, apart from

Table 5.3 Estimates from the classical-approach.[1]

Trait	$\hat{\sigma}_A^2$	$\hat{\sigma}_c^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_P^2$	$\hat{h}^2$
Growth rate, g/d	2,583 ± 249	868 ± 70	3,820 ± 141	7,272 ± 133	0.36 ± 0.03
Back fat thickness, mm	2.83 ± 0.23	0.28 ± 0.05	4.67 ± 0.14	7.78 ± 0.13	0.36 ± 0.03
Muscle depth, mm	7.94 ± 0.76	1.09 ± 0.21	23.07 ± 0.52	32.10 ± 0.48	0.25 ± 0.02
Feed intake, g/d	41,275 ± 3,384	15,201 ± 2,019	39,749 ± 6,050	96,226 ± 2,982	0.41 ± 0.04

[1] Estimates were obtained using Model 1 (Equation 6); ± indicate standard errors of estimates.

effects accounted for in the model such as restricted vs. ad libitum feeding. The pen effects, therefore, seemed to originate from the individuals within the pen, rather than from external factors, suggesting substantial social effects. Thus our results suggest that including pen effects in the model may be essential to avoid biased estimates of genetic parameters, even when pens are fully standardized.

For growth rate and feed intake, a likelihood ratio test with two 2 d.f. strongly favored Model 3 over Model 2 (p << 0.001). Model 3 yielded highly significant social genetic variances for growth rate and especially for feed intake, whereas estimates for back fat thickness and muscle depth were small and nonsignificant (Table 5.5). Estimated direct genetic variances were little affected by including heritable social effects in the model. When judged by their absolute values, estimates of $\sigma_{A_S}^2$ for growth rate and feed intake may seem small. However, because an individual's SBV affects each of its $n-1$ pen mates, small absolute values of $\sigma_{A_S}^2$ may still contribute substantially to heritable variance (σ_{TBV}^2, Equation 4). Heritable variance was 71% of phenotypic variance for growth rate, and 70% of phenotypic variance for feed intake (T^2, Table 5.5). These values are well outside the usual range of heritabilities for those traits (Clutter and Brascamp, 1998), indicating that social effects create additional heritable variance. Comparing Tables 5.4 and 5.5 shows that heritable variance expressed relative to phenotypic variance, $T^2 = \sigma_{TBV}^2 / \sigma_P^2$, was almost three-fold greater than classical heritability for growth rate, and almost four-fold greater than classical heritability for feed intake. Those results show that social effects contribute the vast majority of heritable variance in growth rate and feed intake in this population. The standard error of T^2 for feed intake was large compared to other traits. This is due to the smaller number of observations and the large contribution of social genetic effects, which were estimated with lower precision.

Estimated genetic correlations between direct and social genetic effects were positive but mostly non-significant ($\hat{r}_{A_{DS}}$, Table 5.5). This result suggests absence of

conflict between self interest and interest of others, indicating that heritable interactions were not competitive, but rather neutral or slightly cooperative. When this is the case, classical mass selection for growth rate or feed intake would not increase competition among animals.

Including heritable social effects reduced estimated pen effects (Table 5.4 vs. 5.5). As argued above, pen effects seemed to originate from social interactions among individuals, rather than from physical differences among pens. In Table 5.4, pen effects originate from both heritable and non-heritable social effects, whereas in Table 5.5 heritable social effects are included in $\sigma_{A_S}^2$ and $\sigma_{A_{DS}}$, thus reducing estimated pen effects.

In the statistical analyses of growth rate, feeding strategy was included as a fixed effect, which accounts for differences in mean growth rate between both treatments. However, different feeding strategy may create differences not only in mean but also in variance. We, therefore, split the data into two subsets, one for each feeding strategy, and analyzed both subsets separately (last two rows in Table 5.5). Residual variance for growth rate differed significantly between feeding strategies, being largest with restricted feeding. Apparently, competition for limited resources in restricted fed pens increases differences in growth rate among individuals.

Validation

Analyses always converged to the same results, irrespective of starting values used in ASREML. (Unless starting value were so extreme that convergence failed totally). Details on model comparisons are in the Appendix; here we summarize main results. In mammals, confounding of genetic and environmental effects occurs mostly via the dam. We, therefore, fitted a sire model, so that information on genetic parameters comes entirely via paternal relationships (Lynch and Walsh, 1998). Compared to Table 5.5, the sire model yielded similar direct genetic variance and higher social genetic variance in growth rate (66 vs. 51). The full data used for Table 5.5 was a mix of individuals descending from different sire and dam lines (see 5.3 Material). To investigate a potential bias due to this mixture of lines, we analyzed the subset of individuals descending from the single largest sire line (line H, Table 5.1). Compared to Table 5.5, this analysis yielded a slightly higher social genetic variance in growth rate (71 vs. 51). In the full data, pen size varied from 6 through 12. To investigate a potential effect of varying pen size, we analyzed the data subset for the most frequent pen size (n = 8). Compared to Table 5.5, this analysis yielded a higher social genetic variance (73 vs. 51). In summary, all models

Table 5.4 Estimates from the classical-approach including random pen effects.[1]

Trait	$\hat{\sigma}_A^2$	$\hat{\sigma}_c^2$	$\hat{\sigma}_g^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_P^2$	$\hat{h}^2$
Growth rate, g/d	1,780 ± 172	259 ± 43	1,929 ± 90	3,057 ± 101	7,023 ± 122	0.25 ± 0.02
Back fat thickness, mm	2.79 ± 0.23	0.18 ± 0.05	0.44 ± 0.05	4.37 ± 0.14	7.78 ± 0.13	0.36 ± 0.02
Muscle depth, mm	7.69 ± 0.74	0.86 ± 0.21	1.03 ± 0.18	22.44 ± 0.51	32.02 ± 0.47	0.24 ± 0.02
Feed intake, g/d	17,678 ± 3,244	2,689 ± 1,092	41,018 ± 3,346	35,780 ± 1,986	97,165 ± 3,573	0.18 ± 0.03

[1] Estimates were obtained using Model 2 (Equation 7); ± indicate standard errors of estimates.

investigated yielded a highly significant social genetic variance in growth rate, mostly close to that in Table 5.5, but occasionally higher.

Analysis of variance was used to evaluate the ability of the estimated classical breeding values vs. estimated direct and social breeding values to predict missing records (see 5.4 Methods). When estimated DBV and SBV were not included in the model, estimated classical breeding values were highly significant (p < 0.0001). This result shows that estimated classical breeding values were meaningful in the absence of estimated DBV and SBV. However, when fitting both estimated classical breeding values and estimated DBV and SBV, classical breeding values were no longer significant (p = 0.09), whereas estimated DBV and SBV were highly significant (p = 0.0018 for DBV; p < 0.0001 for SBV). Those results confirm significance of social genetic effects.

The analysis of independent data yielded the following results for growth rate: $\hat{\sigma}_{A_D}^2 = 1,319 \pm 175$, $\hat{\sigma}_{A_S}^2 = 41 \pm 7$, $\hat{\sigma}_{A_{DS}} = -21 \pm 25$, $\hat{\sigma}_{A_{TBV}}^2 = 3,294 \pm 492$ and $\hat{\sigma}_P^2 = 7,012 \pm 134$, so that $\hat{h}_D^2 = \sigma_{A_D}^2/\sigma_P^2 = 0.19$ and $T^2 = 0.47 \pm 0.06$. This shows that T^2 was more than two-fold greater than classical heritability, which is in line with Table 5.5.

5.6 Discussion

Our results demonstrate that social effects may contribute the vast majority of heritable variation in some quantitative traits in mammals. Heritable variances in growth rate and feed intake were more than two-fold greater than suggested by classical heritability. Estimated social genetic variances for growth rate and feed intake were highly significant, which was confirmed by extensive model comparison and independent data. Our results, therefore, demonstrate that

Table 5.5 Estimates when including heritable social effects.[1]

Trait	$\hat{\sigma}^2_{A_D}$	$\hat{\sigma}^2_{A_S}$	$\hat{\sigma}_{A_{DS}}$	$\hat{\sigma}^2_{TBV}$ [2]	$\hat{\sigma}^2_c$	$\hat{\sigma}^2_g$	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_P$ [3]	$\hat{T}^2$	$\hat{r}_{A_{DS}}$ [6]
Growth rate, g/d	1,522 ± 157	51 ± 9	56 ± 27	5,208 ± 669	236 ± 42	1,371 ± 102	3,221 ± 96	7,324 ± 162	0.71 ± 0.08	0.20 ± 0.10
Back fat thickness, mm	2.75 ± 0.23	0.009 ± 0.004	-0.003 ± 0.023	3.19 ± 0.38	0.16 ± 0.05	0.38 ± 0.06	4.36 ± 0.15	7.79 ± 0.13	0.41 ± 0.04	-0.02 ± 0.15
Muscle depth, mm	6.68 ± 0.51	0.027 ± 0.015	0.14 ± 0.07	10.35 ± 1.33	0.85 ± 0.21	0.66 ± 0.28	23.13 ± 0.53	32.17 ± 0.49	0.32 ± 0.04	0.33 ± 0.21
Feed intake, g/d	16,950 ± 3,247	596 ± 240	1,215 ± 695	68,687 ± 17,990	2,620 ± 1,087	28,909 ± 4,043	37,080 ± 1,918	98,535 ± 4,096	0.70 ± 0.17	0.38 ± 0.22
Growth rate, restricted [4]	1,608 ± 188	71 ± 13	59 ± 35	6,466 ± 642	203 ± 57	1,131 ± 125	3,343 ± 120	7,593 ± 195	0.85 ± 0.11	0.18 ± 0.11
Growth rate, ad libitum [5]	1,784 ± 271	62 ± 16	51 ± 51	6,014 ± 1,141	209 ± 83	1,104 ± 215	2,617 ± 163	6,854 ± 214	0.88 ± 0.22	0.15 ± 0.14

[1] Estimates were obtained using Model 3 (Equation 8); ± indicate standard errors of estimates.
[2] From Equation 4 with pen size (n) of 8.5.
[3] From an extension of Equation 2, $\sigma^2_P = \sigma^2_{A_D} + \sigma^2_{E_D} + (n-1)(\sigma^2_{A_S} + \sigma^2_{E_S}) + (n-1)r\left[2\sigma_{A_{DS}} + (n-2)\sigma^2_{A_{SJ}}\right] + \sigma^2_c + \sigma^2_g$, with pen size (n) of 8.5 and average relatedness within pens (r) of 0.18.
[4] Subset of data with restricted fed animals only, # = 9,541 obs.
[5] Subset of data with ad libitum fed animals only, # = 4,491 obs.
[6] Estimated genetic correlation between direct and social effects.

heritable social effects are not merely of theoretical interest, but have significant biological relevance in a real population. Because response to selection is proportional to standard deviation in TBV, potential response in growth rate and feed intake in this population is substantially larger than suggested by classical heritability ($\Delta \overline{P} = \iota \rho \sigma_{TBV}$; Ellen et al., 2007). The increases in heritabilities found are in line with large responses to selection found by Craig and Muir (1996).

Growth rate and feed intake are strongly influenced by social interactions while back fat thickness and muscle depth show only a small increase in heritability. Since carcass weight is part of the statistical model for back fat thickness and muscle depth, these traits describe carcass composition rather than quantity. Our results therefore indicate that carcass composition is little affected by social interactions.

Previous results

Few studies have reported genetic variance in social effects. Bijma et al. (2007b) and Ellen et al. (2008) reported significant social genetic variance in laying hens. Arango et al. (2005) attempted estimation of direct and social genetic parameters for growth rate in a population of 4,946 female finishing pigs. However, due to the data structure in that study, accurate estimation of social genetic variance was impossible, resulting in a nearly flat likelihood and spurious convergence. Van Vleck et al. (2007) estimated direct and social genetic effects for growth rate in a population of 1,882 feed lot bulls. For most of their results, social genetic effects were non-significant, which is not surprising given their small data set of a few large pens. With few pens, it is difficult to discriminate between heritable and non-heritable effects, because heritable and non-heritable social genetic covariances among individuals are fully confounded within pen. Chen et al. (2006) estimated genetic parameters of direct and social genetic effects for growth rate in a population of 11,235 pigs, kept in pens of 15 individuals. Though the authors did not report significance levels, log-likelihoods values presented in their results suggest significant social genetic variance. As in the present study, Chen et al. (2006) observed a substantial increase in estimated direct heritability when group effects were omitted from the model, suggesting that their groups consisted partly of relatives.

The contribution of social effects to heritable variance is often misjudged. Both Van Vleck et al (2007) and Chen et al (2006) judged their estimated $\sigma^2_{A_S}$ as small, not realizing its substantial contribution to total heritable variance. When comparing total heritable variance calculated from their results to classical heritabilities, the following results are obtained: $T^2 = 1.42$ vs. $h^2_D = 0.14$ (Van Vleck et al., 2007, Table 5.3, period 1, Models 1 and 5), and $T^2 = 0.58$ vs. $h^2_D = 0.29$ (Chen et al. 2006,

Table 5.3, scheme 1a). Though those results were not always significant, such values are large rather than small.

Remarkably, some studies referred to social effects as "competitive effects", even when estimated genetic correlations between direct and social genetic effects were positive (Arango et al., 2005; Chen et al., 2006; Van Vleck et al., 2007). A positive correlation, however, indicates that individuals with positive direct effects also have positive social effects on average, indicating mutual benefit rather than competition.

Estimability

Van Vleck and Cassaday (2005) used simulated data to investigate estimability of social genetic effects. They showed that estimates depended heavily on whether or not group effects were included in the model, and whether group effects were treated as fixed or random. Analyses without group effects yielded substantially overestimated social genetic variance, but the cause of this phenomenon was left unclear. In 5.4 (Methods), we show that group effects take account of non-heritable social effects ($\sigma_{E_S}^2 > 0$). Our simulations confirmed that the expected between-group variance equals $2\sigma_{E_{DS}} + (n-2)\sigma_{E_S}^2$, illustrating that non-heritable social effects translate into between-group variance (results not shown). Because heritabilities are rarely close to 100%, it is unlikely that social effect are fully heritable (i.e., $\sigma_{A_S}^2 > 0$ while $\sigma_{E_S}^2 = 0$). Therefore, when analyzing social genetic effects, one should always account for a non-heritable component, either by allowing residuals to be correlated within groups, or by including random group effects when n is large.

Because between-group variance originates from non-heritable social effects, which are random effects, group effects should ideally be fitted as random rather than fixed. Van Vleck et al (2007) and Cheng et al (2006) observed that analysis with groups included as fixed effect failed, which also occurred in our analysis. Our simulations, in contrast, showed that genetic parameters are identifiable and estimates are unbiased when groups are treated as fixed and are composed fully at random with respect to family (results not shown). In our data, however, groups were partly composed of family members, which probably explain failure when including group as fixed effect.

When group members are related, social genetic variance may not be identifiable. For example, the appendix of Bijma et al. (2007b) shows that the data structure used by Wolf (2003) prohibits identification of the social genetic variance. Estimation of social genetic effects seems most powerful when populations consist

of many small groups of unrelated individuals, but more research on optimum designs is needed.

Animal breeding

Animal breeders can utilize heritable social effects to increase response in their selection programs. Griffing (1967; 1976) showed that breeding schemes need to be adapted to improve socially affected traits (see also Muir 2005). One strategy to fully utilize heritable variance, is to use groups composed of family members when recording phenotypic data. With this strategy, one may either keep selection candidates themselves in family groups, such as in classical group selection (e.g., Griffing, 1976), or keep relatives of selection candidates in family groups and select among candidates based on performance of their relatives. For example, Ellen et al. (2007) showed that accuracy of selection based on information of progeny kept in family groups has a maximum of 100%, whereas maximum accuracy was lower or even negative when progeny were kept in groups of unrelated individuals. Thus, animal breeders may use 'artificial kin selection' to improve socially affected traits. Selection based on sib or progeny information does not require knowledge of direct and social genetic variances. When direct and social genetic variances are known, however, such as for the current pig population, selection on Best Linear Unbiased Predictions (BLUP, Henderson 1975) of TBVs may yield higher response, or allow for different population structures. For example, Muir (2005) used simulated data to show that selection using BLUP yielded higher responses than group selection with groups composed of full sibs.

Social behaviors may depend on environmental circumstances. With restricted feeding on pen level, competition for a fixed total amount of feed creates negative correlations between individual intakes within pens, causing a negative correlation between direct and social effects. Unfortunately, individual feed intake was not recorded with restricted feeding. Because growth rate and feed intake are highly genetically correlated (r_g = ~0.65; Clutter and Brascamp, 1998), one might expect restricted feeding to cause a negative genetic correlation between direct and social effects on growth rate. For both feeding strategies, however, genetic correlations were non-significant, suggesting that competition for finite resources on the phenotypic level does not necessarily translate to the genetic level.

Long-term selection

Classical traits not affected by social interactions often continue to respond to selection for many generations, indicating that selection does not exhaust heritable variance (e.g., Dudley and Lambert, 2004). It is unclear whether this observation

extends to socially affected traits. Once social effects are on a 'sufficient' level, further improvement of social behaviors may not translate into response in trait value. For example, once tree breeders would manage to breed individuals maintaining equal height, thus cancelling competition for daylight, further increase in productivity by decreasing competition for day light seems difficult. In quantitative genetic analysis, this phenomenon would surface as gradually decreasing social genetic variance. On the one hand, this would be undesirable because it reduces opportunities for further genetic improvement. On the other hand, however, a reduction in social genetic variance would increase uniformity of individuals, which is often desirable but has been difficult to achieve in livestock (SanCristobal et al., 1998; Hill and Zhang, 2004)

Social effects on kin

Hamilton proposed kin selection as a mechanism for the evolution of social behaviors (Hamilton, 1964). Kin selection may cause individuals to behave more cooperatively towards relatives compared to non-relatives, because helping relatives has inclusive fitness benefits (e.g., Frank, 1998). To investigate whether relatedness among individuals affected trait values in the current population, we included a linear regression of growth rate on mean additive genetic relatedness within pen in Model 3 (Equation 8). The estimated regression coefficient equaled 29 g/d (p < 0.10), meaning that a pen of full sibs (r = ½) shows 15 g/d higher growth rate than a pen of non-relatives. The 15 g/d corresponds to ~0.2 phenotypic standard deviation, indicating a moderate effect. We are currently investigating the origin of this effect. Including a regression on relatedness hardly affected estimated direct and social genetic parameters (results not shown).

Natural populations

For natural populations, collecting sufficient data involves substantial effort, and often yields data structures that are difficult to analyze. Animal and plant breeders have developed flexible statistical tools, such as the so-called animal model, which may be useful for studying natural populations (e.g. Kruuk 2004). Statistical methods presented in Muir (2005) and Bijma et al. (2007b) do not require balanced designs or specific family relationships within groups. Moreover, those methods enable estimating social genetic variance without the need to record the behavior per se. For example, as illustrated in the present paper, those methods allow estimating social genetic variance in growth rate without recording behavioral interactions among group members. Compared to behavioral studies, this represents a substantial saving of labor, which may be used to collect information

on a larger number of individuals, so as to enable quantitative genetic analysis of meaningful accuracy. Application of an animal model requires i) knowledge of which individuals interact with each other (i.e. the identification of groups), ii) phenotypic records on the trait of interest, and iii) additive genetic relatedness among all individuals. When pedigrees are unknown, additive genetic relatedness may either be estimated directly from molecular markers (Lynch and Ritland, 1999; Toro et al., 2002; Oliehoek et al. 2006), or the pedigree may be reconstructed using molecular markers (Blouin, 2003). When DNA-samples are available on multiple generations, pedigree reconstruction provides information on the number of offspring of individuals, i.e. on their fitness. Such information may be used to estimate total heritable variance in fitness, the contribution of social effects to total heritable variance, and the genetic correlation between direct and social genetic effects on fitness. Knowledge of this correlation would reveal the strength of heritable competition within species, and the degree to which such competition constraints evolutionary success of the species.

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Appendix

Phenotypic variance

From Equation 1, $Var(P) = Var[A_{D,i} + E_{D,i} + \sum_{j\neq i}^{n-1}(A_{S,j} + E_{S,j})]$. With $Cov(A, E) = 0$ for all i, j, and $Cov(E_{D,i}, E_{S,j})$ when $i \neq j$, it follows that $Var(P) = \sigma_{A_D}^2 + \sigma_{E_D}^2 + Var(\sum_{i\neq j}^{n-1} A_{S,j}) + Var(\sum_{i\neq j}^{n-1} E_{S,j}) + 2Cov(A_{D,i}, \sum_{i\neq j}^{n-1} A_{S,j})$. With $Cov(A_{S,j}, A_{S,j'}) = r_{jj'}\sigma_{A_S}^2$ in which $r_{jj'}$ is relatedness between individuals j and j', it follows that $Var(\sum_{i\neq j}^{n-1} A_{S,j}) = (n-1)\sigma_{A_S}^2 + (n-1)(n-2)r\sigma_{A_S}^2$, r denoting mean relatedness within groups. Furthermore, with $Cov(E_{S,j}, E_{S,j'}) = 0$ when $j \neq j'$, $Var(\sum_{i\neq j}^{n-1} E_{S,j}) = (n-1)\sigma_{E_S}^2$. Finally, $Cov(A_{D,i}, \sum_{i\neq j}^{n-1} A_{S,j}) = (n-1)r\sigma_{A_{DS}}$. Collecting terms yields $\sigma_P^2 = \sigma_{A_D}^2 + \sigma_{E_D}^2 + (n-1)(\sigma_{A_S}^2 + \sigma_{E_S}^2) + (n-1)r[2\sigma_{A_{DS}} + (n-2)\sigma_{A_S}^2]$, which is Equation 2.

Validation

To evaluate robustness of our estimates, we performed additional analyses for growth rate (Table A5.1). The row 'Basic' in Table A5.1 corresponds to results in Table 5.5. We distinguished four possible sources of bias:

1. Due to imperfection of the statistical model, genetic and non-genetic effects might be confounded.
2. Our data was a mix of individuals from a large number of crosses (Table 5.1), which might affect results.
3. For part of our data, all animals within a pen were slaughtered at the same day, whereas for the remaining part of the data, delivery decisions were based on individual body weight. As a result, interval between delivery of the first and last animal within a pen lasted up to 4 weeks.
4. Pen size varied between 6 and 12 individuals, which may affect estimates.

Confounding

Early life experience may affect social behaviors later in life. As a consequence, individuals born in the same litter may show similar social effects, leading to non-genetic covariances between social effects of full sibs. When not accounted for in the statistical analyses, such effects would inflate estimated social genetic variance. To reduce this risk, we performed two additional analyses. First, we applied a sire model, so that covariances between pen mates of full sibs do not contribute to estimated social genetic variance. Results of the sire model strongly supported presence of social genetic variance (p < 0.001, 'Sire model', Table A5.1). Second, we

Table A5.1 Estimates (± standard error) for growth rate from different models.

Model	$\hat{\sigma}^2_{A_D}$	$\hat{\sigma}^2_{A_S}$	$\hat{\sigma}_{A_{DS}}$	$\hat{\sigma}^2_c$	$\hat{\sigma}^2_{foster}$	$\hat{\sigma}^2_{common-social}$	$\hat{\sigma}^2_g$	$\hat{\sigma}^2_e$
Basic	1,522 ± 157	51 ± 9	56 ± 27	236 ± 42	-	-	1,371 ± 102	3,221 ± 96
Sire model[1]	1,698 ± 267	66 ± 14	117 ± 43	573 ± 49	-	-	1,625 ± 83	3,947 ± 54
Basic incl. social common env.	1,525 ± 157	49 ± 9	54 ± 27	229 ± 42	-	12 ± 6	1,318 ± 104	3,205 ± 96
Foster in stead of common	1,609 ± 151	50 ± 9	49 ± 27	-	290 ± 38	-	1,377 ± 102	3,096 ± 95
Both common and foster	1,506 ± 155	49 ± 9	52 ± 27	106 ± 45	249 ± 41	-	1,365 ± 102	3,131 ± 95
Only 1 sire line, ♂H; (# = 3927 obs.)	1,653 ± 384	71 ± 21	34 ± 59	259 ± 118	-	-	1,149 ± 210	3,399 ± 229
Different error variances per sire line	1,514 ± 156	50 ± 9	58 ± 27	238 ± 42	-	-	1,374 ± 102	3,212 [2]
Different error variances per cross	1,531 ± 156	50 ± 9	56 ± 27	223 ± 41	-	-	1,369 ± 102	3,224 [2]
Delivery based on weight; (# =8129 obs.)	1,648 ± 200	44 ± 10	37 ± 33	169 ± 48	-	-	1,007 ± 114	2,906 ± 122
Only 8-animal pens; (# = 5523 obs.)	1,684 ± 247	73 ± 18	67 ± 47	188 ± 84	-	-	932 ± 173	3,189 ± 158

[1] For the sire model, genetic variance components were calculated as four times the corresponding sire component (Lynch and Walsh, 1998).
[2] Weighed average.

fitted a non-genetic social effect common to individuals born in the same litter. For this purpose, we fitted the litter-id of an individual as a non-genetic effect in the records of its pen mates. This is an analogy of a classical common-environmental effect, but in this case it refers to social effects rather than direct effects. Results showed a small but significant variance for the common social effect of litter mates ($p < 0.05$, 'Basic incl. social common env.', Table A5.1), suggesting that early life experiences affect social behaviors. Estimated social genetic variance was not affected by including social common environment effects.

The basic model included a common environment among littermates. However, because at least 25% of individuals were cross-fostered, common environment due to the foster sow might affect estimates. Therefore, a model including common environment due to the foster sow, instead of the biological mother, was fitted ('Foster in stead of common', Table A5.1) as well as a model including both effects ('Both common and foster', Table A5.1). Both effects were highly significant, but estimated genetic variance components were unaffected.

To account for a within group non-genetic correlation, we included a random pen effect (see Methods). We also evaluated an alternative model in which pens were treated as fixed effects, while omitting number of pen mates, gender, feeding strategy and compartment, because of full confounding. This analysis converged, but variance components for social effects could not be estimated due to singularity (see Discussion).

Multiple crosses

The full data consisted of crossbred individuals descending from multiple sire and dam lines. A sire model ignores existence of multiple dam lines. Results of the sire model, therefore, indicate that significant social genetic variance was not an artifact caused by multiple dam lines underlying the observed data ('Sire model', Table A5.1). To further investigate the effect of multiple parental lines, we analyzed the sub set of data originating from the largest cross using Model 3 ($\male$H x $\female$A; n = 1,417; Table 5.1). However, this analysis did not converge, probably due to the small number of observations. We, therefore, analyzed the next best alternative, which was the sub set of individuals descending from the single largest sire line, but from multiple dam lines ('Only 1 sire line, $\male$H; n = 3,927, Table A5.1). Results confirmed previous finding.

Analyses thus far assumed that residual variances did not depend on the cross. We investigated two alternatives allowing for heterogeneous residual variances; the first allowing for different residual variances per sire line ('Different error variances per sire line', Table A5.1), and the second allowing for different residual variances

per cross ('Different error variances per cross', Table A5.1). Results were nearly identical to those in Table 5.5.

Delivery strategy
To investigate a potential effect due to delivery per pen versus delivery based on individual weight, we analyzed the sub set of data on individuals delivered based on individual weight (Delivery based on weight, Table A5.1). Estimated genetic parameters were in line with Table 5.5.

Pen size
To investigate a potential effect due to varying pen size, we analyzed the sub set of data of the single most frequent pen size (Only 8 animals per pen, Table A5.1). Estimated social genetic variance was greater than in Table 5.5 (73 vs. 51), but the difference was not significant.
In conclusion, all of the above analyses strongly support presence of heritable variance due to social effects.

6

Genetic correlations between lactation performance and growing-finishing traits in pigs

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Abstract

Genetic selection for increased litter size of sows increases the risk of a large negative energy balance during lactation. Furthermore, the feed intake capacity of the lactating sows might be reduced due to the simultaneous selection for higher feed efficiency during the growth phase when the sows were actually reared as finishers but later on selected for breeding. There is a need to improve lactation performance of sows while continuing selection for feed efficiency of grower-finishers in commercial breeding. Therefore, this study was conducted to estimate genetic correlations between growing-finishing traits and lactation performance traits. An additional objective was to study the impact of including additive social effects in the animal model on the genetic correlation estimates. Analyses were performed on a population of 1,149 commercial crossbred sows with repeated observations on lactation performance traits and their 7,723 grower-finishers-offspring.

The genetic correlation between daily gain of grower-finishers and starting weight of lactating sows was positive (r_g=0.24; $p<0.05$). The correlation between off test back fat of grower-finishers and fat mass of lactating sows was also positive (r_g=0.53; $p<0.05$). The genetic regulation of feed intake from the beginning of lactation seems to differ from the genetic regulation of feed intake during the growing-finishing period as the correlation between these two traits was low (r_g=+0.23; $p<0.05$). Feed efficiency during growing-finishing and lactation phases showed similar tendencies as the genetic correlation between residual feed intake of the grower-finisher and lactation efficiency of sows was -0.51 ($p<0.05$). Taking heritable social effects into account for daily gain and feed intake did not affect the genetic correlation estimates, neither within growing-finishing traits nor between growing-finishing traits and lactation performance traits.

It was concluded that selection for growing-finishing traits in dam lines could be combined with selection for lactation performance traits.

Key words: Genetic parameters, Lactating sows, Growing-finishing traits, Social effects

6.1 Introduction

Litter size of sows has increased over the past decade through genetic selection and improved environment (Pigchamp, 2010). However, milk production of sows has to keep up the pace with increased litter size to maintain piglet growth and piglet survival until weaning. Further, feed intake of sows during lactation is often not high enough to sustain the increased milk production needs (Eissen, 2000).

In the Netherlands, like most other countries, almost 65% of the total production costs of a slaughter pig originate from the growing-finishing phase (Landelijk biggenprijzenschema, 2010). Hence, it is economically worthwhile to include growing-finishing characteristics in a breeding objective for dam lines. However, additional selection for growing-finishing traits in dam lines is often expected to negatively affect feed intake and/or body tissue mobilization of lactating sows. The hesitation in selecting for leanness and feed efficiency in sows is based on the expectation that grower-finisher traits show a moderate to high genetic correlation with the corresponding traits when the pig is actually raised as a lactating sow. However, no research was found to confirm this hypothesis.

Recently, a novel 'group selection' method has been designed which considers both the performance of an individual, and its heritable social effect on performance of group members, by adding a 'social breeding value' to the genetic model (Bijma et al., 2007a). Bergsma et al. (2008a) demonstrated that daily gain and feed intake of finishing pigs are affected by heritable social interactions among group members. Social interactions between pigs profoundly affect their welfare and performance. If improvement of social interactions becomes part of the breeding objective one might expect that animals spend less energy on fighting and stress and thus become more efficient. Adoptation of this new methodology might change the genetic correlations. Therefore, it is useful to include social effects in estimation of genetic correlations between the growing-finishing and lactation traits.

This study was conducted to estimate genetic correlations between lactation performance traits and growing-finishing traits. In addition, the impact of including additive social effects in the model for estimating the genetic correlations was evaluated.

6.2 Material and methods

Animal were subjected to standard production conditions and no additional measurements were taken. Consequently no approval of the Care and Use

Committee approval was needed. Observations from two farms were used in this study. Both these farms, the experimental farm of IPG and the experimental farm of ASG are operating in line with the regulations of the Dutch law on protection of animals.

Datasets

The data consisted of records from two farms. The first dataset was from the experimental farm of IPG. Records on commercial sows from TOPIGS (Vught, The Netherlands) and their offspring were used. The second dataset was from the experimental farm 'Sterksel' of the Animal Sciences Group (ASG) of Wageningen UR. At ASG, effects of a low protein and low phosphorus gestation diet (by phase feeding) on reproductive performance, stayability and mineral excretion were studied during four successive parities (van der Peet-Schwering et al., 2005). Sows on both farms partly have a common pedigree.

The number of observations differed considerably according to the trait. Feed intake during lactation was recorded on 1,149 sows. These sows descended from 187 sires and 548 dams. There were 7,176 animals with records on feed intake during growing-finishing period. They descended from 528 sires and 623 dams. Out of these 623 dams, 577 had their own record on feed intake during lactation. Feed intake data and related observations on growing-finishing characteristics were available for up to 27,615 pigs from the IPG- farm. The mothers of these grower-finishers did not have an observation on grower-finisher characteristics themselves. Pedigree records on three generations of parents were available. A total of 33,764 animals were included in the pedigree file.

Feeding strategy

At the ASG-farm, sows were fed *ad lib.* At the IPG-farm, a computerized feeding schedule was used to avoid wastage of feed by sows. Maximum allowance for primiparous sows was 7 kg/d and 8 kg/d for multiparous sows. Primiparous sows at the IPG-farm were fed *ad lib* for a certain period of time as well. The sows on *ad lib* diet were fed according to an ascending scale from parturition until day six after parturition, and were given free access to the lactation diets from day six after parturition onwards. The computerized feeding schedule took 14 days to achieve the maximum daily feed allowance. At both farms, a commercial lactation diet was fed to sows during lactation.

In a previous study (Bergsma et al., 2009), phenotypic relations between underlying traits of lactation performance, and phenotypic relations between lactation performance and reproductive traits were remarkably similar for the two farms,

even though the ASG-farm fed ad libitum during lactation and the IPG-farm truncated feed allowance. Of the IPG-farm, the period in which primiparous sows were fed *ad lib*, was omitted in that study. In another study (Bergsma et al., 2008b) using a, to a large extend overlapping dataset compared to this study, the genetic correlation between *ad lib* feed intake during lactation and truncated feed intake, was estimated at +0.83 (± 0.44). The unweighed average over parity one to four was 5.17 kg/d for both feeding strategies. The standard deviation was similar as well (0.73 kg/d for ad lib fed sows and 0.70 kg/d for truncated feed intake). Therefore, in the current study, observations of the two dataset were treated as one dataset. *Ad lib* and truncated feed intake during lactation were treated as one trait as well.

The use information on crossbred animals
In the first dataset, from the experimental farm of IPG, commercial TOPIGS crossbred sows (Vught, The Netherlands) and their offspring by different commercial sire lines were used. The sows were crosses from four lines used in a common genetic evaluation program. There are genetic differences between lines and some heterosis effects especially for reproduction traits. However, as a common practice in many large scale genetic evaluation systems, the different lines were used in one animal model genetic evaluation system accounting for differences between lines. The use of crossbred data and the related non-additive effects could have some effects on the estimates of the breeding values. However, the volume and information in the crossbred data also provided additional opportunities for more accurate estimations relevant to actual commercial environments. A combined crossbred and purebred selection (CCPS) method, i.e. using crossbred and purebred information, is optimal for obtaining genetic response in crossbreds (Ming Wei and van der Werf, 1994). Further, it was assumed that the genetic relationship between the traits of interest were not affected by use of crossbred information as the non-additive effects are expected to have lesser effect on genetic correlations compared to genetic evaluations for individual traits.

Lactation performance traits
Lactation performance is used in this study as a collective noun for seven different traits. These traits are described below. In addition more information on these traits can be found in Bergsma et al. (2009).
Starting weight for the lactation period (the body weight of a sow shortly after parturition) was estimated from the weight of the sow at the time of transfer to

the farrowing house (pre-partum observation), weight of her live- and stillborn piglets at birth (post-partum observation) and the estimated weight of the placenta and intra-uterine fluids. It was assumed that the sow herself did not gain or loose weight during the short period between transfer to the farrowing house and parturition. Fat mass at start of lactation was estimated from her starting weight and backfat thickness. Backfat thickness was recorded ultrasonically together with weight at the time of transfer to the farrowing house. At weaning, weight of each sow was recorded again. Weight loss was estimated by subtracting body weight at weaning from starting weight. Litter weight gain was recorded as the weight of the piglets at weaning minus the sum of the birth weights of the piglets after cross fostering. Lactation efficiency was defined as an energy efficiency of sows, and was calculated as

output (×100%) / input.

Input was calculated as:

Input, MJ of ME/d = (energy from total feed intake during lactation
+ energy from body fat mobilization of the sow
+ energy from body protein mobilization of the sow
− energy needed for maintenance of the sow)
÷ lactation length.

Output during lactation was calculated as:

Output, MJ of ME/d = (energy in fat deposition of live piglets at weaning
+ energy in protein deposition of live piglets at weaning
+ energy in fat deposition of dead piglets
+ energy in protein deposition of dead piglets
+ energy needed for maintenance of weaned piglets
+ energy used for maintenance of piglets that died before weaning)
÷ lactation length.

Both energy input and output were estimated per sow per day averaged over the lactation period. All energy units were expressed in MJ Metabolisable Energy (ME).

Growing-finishing traits
Replacement gilts at the IPG-farm were bought and not performance tested. Growing-finishing traits were recorded for the offspring. About one third of the growing-finishing pigs were fed ad libitum using IVOG feeding stations to record

individual feed intake. The remaining two-thirds of the growing-finishing pigs were fed restrictedly at group level during the entire growing-finishing period. Individual feed intake was not recorded for restricted fed animals. On pen level, restricted feed intake was about 90% of feed intake in ad libitum fed pens. All growing-finishers were weighed individually at start of the growing-finishing period at about 27 kg. At slaughter, hot carcass weight was recorded along with back fat thickness and muscle depth using the Hennessy Grading Probe. Live weight and ultrasonic backfat thickness was recorded the day before slaughter of the ad libitum fed pigs. From January 2005 onwards, live weight (not ultrasonic backfat thickness) was recorded on restricted fed growing-finishers also.

For the growing-finishing characteristics, five traits of interest were identified: growth rate, back fat thickness, muscle depth, feed intake and feed efficiency. To calculate daily gain, live weight at the end of the trajectory was either measured or calculated based on the slaughter weight. Therefore, two different traits were analyzed: daily gain (live weight minus penning weight, divided by the length of the growing-finishing period) and net daily gain (calculated live weight minus penning weight, divided by the length of the growing-finishing period). The formula to calculate live weight based on the slaughter weight is given in the Appendix. Back fat thickness was either determined ultrasonically on live animals (US back fat in mm), or at slaughter, using the Hennesy Grading Probe (HGP_fat in mm). The Hennesy Grading Probe also measures muscle depth (HGP_muscle in mm). Feed intake was calculated as cumulative feed intake during the growing-finishing period, divided by the length of the growing-finishing period (FI in g/d). As a measure of feed efficiency, residual feed intake was calculated. Residual feed intake was calculated as a linear function of feed intake, production (protein and fat deposition) and maintenance of live weight and as such an attractive characteristic to use to represent production efficiency (for derivation: see Appendix). Residual feed intake and lactation efficiency both estimate the efficiency of the energy metabolism in a similar way. In comparison to residual feed intake, lactation efficiency is a function of feed intake and body tissue mobilization, (milk) production and maintenance of the sow, although, lactation efficiency is expressed as a ratio of output over input.

The number of observations per trait varied considerably; numbers are shown in Table 6.1 along with the mean, standard deviation, minimum and maximum per trait.

Table 6.1 Descriptive statistics (number of observations, mean, standard deviation, minimum and maximum) for traits and covariariates used to estimate heritabilities and genetic correlations.

	No.	Mean	Std	Min	Max
I. Lactation performance traits					
Parity		3.2	2.06	1	12
Lactation length, d		26.6	3.6	14	47
Weight at start, kg	3006	217	35	128.9	313.3
Fat mass at start, kg	2980	44.9	8.7	21.9	80.1
Weight loss during lactation, kg	2776	17.0	14.2	-31.0	66.1
Feed intake during lactation, kg	3917	137	30.8	36.3	307.0
Litter weight gain, kg	3401	65.1	15.1	1.7	136.9
Lactation efficiency, %	2202	71	14.2	27	150
II. Growing-Finishing traits					
On test weight, kg		27.1	6.6	7.8	63.5
Off test weight, kg		113.7	8.1	63.0	147.8
Calculated (off test) live weight, kg[1]		113.4	7.4	71.9	149.4
Daily gain, g/d[2]	17372	862	95	496	1233
Net daily gain, g/d[1]	22721	853	91	424	1178
Ultrasonic back fat, mm	8959	13.4	2.5	6.0	22.0
HGP back fat, mm	21727	16.6	3.1	7.6	30.4
HGP muscle depth, mm	21727	57.9	6.2	33.6	84.8
Feed intake, g/d	7723	2156	306	980	3380
Residual feed intake, g/d	7188	26	193	-1069	767

[1] based on hot carcass weight (used to estimate live weight);
[2] based on live weight.

Estimation of Genetic Parameters

Genetic parameters were estimated using restricted maximum likelihood (REML) analyses based on an animal model. For growing-finishing traits, two different models were used. Model 1 was a classical animal model:

$$y = Xb + Za + Wc + Vg + Uf + e, \qquad (1)$$

in which **y** is the vector of observations; **X**, **Z**, **W, V** and **U** are known incidence matrices; **b** is a vector of so-called fixed effects; **a** is a vector of random additive genetic effects (breeding values), which were assumed to have a normal distribution, $\mathbf{a} \sim N(\mathbf{0}, A\sigma_A^2)$; **c** is a vector of random non-genetic effects common to individuals born in the same litter, with $\mathbf{c} \sim N(\mathbf{0}, I_c\sigma_c^2)$; **g** is the vector of random group effects (animals grouped together in the same pen), $\mathbf{g} \sim N(\mathbf{0}, I_g\sigma_g^2)$; **f** is the vector of random effects common to individuals performance tested in the same

compartment of the barn within the same contemporary group, $\mathbf{f} \sim N(\mathbf{0}, I_f \sigma_f^2)$; and $\mathbf{e}$ is a vector of residuals, with $\mathbf{e} \sim N(\mathbf{0}, I_e \sigma_e^2)$. The I_c, I_g, I_f and I_e are identity matrices of the appropriate dimensions, and $\mathbf{A}$ is a matrix of additive genetic relationships among all individuals.

The second model, Model 2 was used to account for heritable social effects:

$$y = Xb + Z_D a_D + Z_S a_S + Wc + Vg + Uf + e, \tag{2}$$

in which $\mathbf{Z}_D$ and $\mathbf{Z}_S$ are known incidence matrices for direct and social genetic effects, and $\mathbf{a}_D$ and $\mathbf{a}_S$ are vectors of random direct and social genetic effects, with

$$\begin{bmatrix} \mathbf{a}_D \\ \mathbf{a}_S \end{bmatrix} \sim MVN \otimes (\mathbf{0}, \mathbf{C} \otimes \mathbf{A}), \text{ in which } \mathbf{C} = \begin{bmatrix} \sigma_{A_D}^2 & \sigma_{A_{DS}} \\ \sigma_{A_{DS}} & \sigma_{A_S}^2 \end{bmatrix} \text{ and } \otimes \text{ indicates the}$$

Kronecker product of matrices. Other elements were the same as in Model 1. Model 2 was similar to Model 3 (equation 8) of Bergsma et al. (2008a), except for the $\mathbf{f}$-vector which was added to the model in this study. The use of Model 2 or Model 1 was based upon a log-likelihood ratio test.

Because each individual interacts with $n-1$ others, the total heritable impact of an individual on the mean trait value of the population is the sum of individual i 's direct breeding value and $n-1$ times its social breeding value. Bijma *et al*. (2007a), therefore, defined the Total Breeding Value as:

$$TBV_i = A_{D,i} + (n-1)A_{S,i}$$

To express heritable variance relative to phenotypic variance, we use

$$T^2 = \sigma_{TBV}^2 / \sigma_P^2,$$

which is an analogy of $h^2 = \sigma_A^2 / \sigma_P^2$, though T^2 may exceed one. Note that T^2 is not a true heritability, but represents heritable variance expressed on the scale of phenotypic variance among individuals. Comparison of T^2 and classical $h^2 = \sigma_A^2 / \sigma_P^2$ allows quick judgment of the contribution of social effects to heritable variance. c^2, f^2 and g^2 are used to express the variance due to the random common environment, compartment within contemporary group and group effect respectively, relative to phenotypic variance.

A repeatability animal model (Model 3) was used for all lactation performance traits as follows:

$$y = Xb + Za + Wp + e, \hspace{4cm} (3)$$

where **Y** is the vector of observations; **X, Z** and **W** are known incidence matrices; **b** is the solution vector of fixed effects; **a** is the vector of random additive genetic effects (breeding values), which were assumed to follow a normal distribution, $\mathbf{a} \sim N(\mathbf{0}, A\sigma_A^2)$; **p** is the vector of random permanent non-genetic effects of each sow, $\mathbf{p} \sim N(\mathbf{0}, I_p \sigma_p^2)$; and **e** is the vector of the residuals, $\mathbf{e} \sim N(\mathbf{0}, I_e \sigma_e^2)$. I_p and I_e are identity matrices and **A** is the additive genetic relationship matrix.

The data were analyzed with ASREML software (Gilmour et al., 2006). Genetic parameters were estimated in two ways. Univariate analyses were performed to estimate the heritability of all traits as well as for repeatabilities of lactation performance traits. Genetic correlations were estimated using either bivariate or multivariate analyses. Corresponding traits (daily gain and net daily gain; HGP_fat and US_fat) were used together. If these traits were involved, a multivariate analysis was performed, otherwise a bivariate analysis was used.

Different statistical models were used for different traits to obtain maximum accuracy of estimates. The fixed effects included in the vector **b** are given in models a through f (Table 6.2). Only significant effects were included in the models. Effects, for which heritabilities were estimated, were excluded from the models in both the bivariate and multivariate analyses. Significance levels of genetic correlations were estimated using a T-test.

6.3 RESULTS

Growing-finishing traits

Genetic parameters for growing-finishing traits are presented in Table 6.3. The heritable social effects were significant for daily gain, net daily gain and feed intake. Therefore, Model 2 was also used for these traits. Although the definition of daily gain and net daily gain differed, these traits could be considered as one since the genetic correlation between the direct effects was almost one (r_g=+0.97 ± 0.005), as was the genetic correlation between the social effects (r_g=+0.94 ± 0.03). Ultrasonically measured backfat and HGP backfat are similar traits. The genetic correlation between both the direct effects was high (r_g=+0.91 ± 0.02). Ultrasonic backfat was not affected by social interactions. HGP back fat was affected, although the effect was small. Previous analysis (Bergsma et al., 2008a) also did not show social effects for HGP back fat. Therefore, the social effect for backfat was ignored. Because of the high genetic correlations between both characteristics on gain, only

Table 6.2 Fixed effects included in the vector **b** for different traits.

Model	Dependent trait(s) Fixed effects [1]
A	Weight at start of lactation; Fat mass at start of lactation
	μ + PARITY$_j$ + HYS$_k$ + LINE$_l$
B	Weight loss; Feed intake during lactation; Lactation efficiency; Litter weight gain;
	μ + PARITY$_j$ + HYS$_k$ + LINE$_l$ + $b_1 \times$ LLE
C	Daily gain; Net daily gain
	μ + GENDER$_j$+ LINE$_k$ + COMP$_l$
D	HGP fat depth; HGP muscle depth
	μ + GENDER$_j$+ LINE$_k$ + COMP$_l$+ $b_1 \times$CALCLW
E	Ultrasonic back fat thickness
	μ + GENDER$_j$+ LINE$_k$ + COMP$_l$+ $b_1 \times$OFTWT
F	Feed intake (growing-finishing); Residual feed intake (growing-finishing)
	μ + GENDER$_j$+ LINE$_k$ + COMP$_l$+ $b_1 \times$ONTWT

[1] where: PARITY = the parity of the sow. Parity 6 and higher were combined; HYS = Herd-Year-Season = Farm ×month of farrowing; LINE= the line code of the sow for lactation performance traits and line of the animal for growing-finishing traits; LLE = Lactation length; GENDER= the gender of the animal; COMP=Compartment within barn, compartment was confounded with feeding strategy (*ad lib* or restricted).Therefore, COMP also accounts for differences between feeding strategies; CALCLW = Calculated live weight; OFTWT = Off test weight; ONTWT = On test weight.

daily gain (and not net daily gain) will be discussed. For the same reason only ultrasonic backfat (and not HGP backfat) will be discussed. HGP muscle depth and Residual feed intake were not affected by heritable social effects.

There were large effects of contemporary group within compartment (f^2) and group (g^2) for feed intake and residual feed intake. The sum of both, applying Model 1, explained 47% and 46 % of the phenotypic variance of these traits, respectively (Table 6.3). The effect of the common environment among littermates (c^2) explained less than 5% of the phenotypic variance for all traits.

Lactation performance traits

All lactation performance traits showed a repeatability higher than the heritability (Table 6.4), indicating the presence of a permanent environment effect. Especially weight and fat mass at start of lactation both showed a high heritability and repeatability.

Genetic correlations among growing-finishing traits

Genetic correlations among growing-finishing traits are presented in Table 6.5. Daily gain and feed intake were significantly affected by social genetic effects.

Table 6.3 Genetic parameters, heritability (h^2), common environmental effects (c^2), group effects (g^2) and compartment within contemporary group effects (f^2) for growing-finishing traits.

	Model[1]	h^2 / T^2 [2]	c^2	g^2	f^2	σ^2_A / σ^2_{TBV} [2]
Daily gain, g/d[3]	1	0.24	0.04	0.11	0.17	1,843 ± 148
	2	0.34	0.04	0.09	0.16	2,654 ± 346
Net daily gain, g/d[4]	1	0.22	0.04	0.11	0.17	1,473 ± 118
	2	0.32	0.04	0.10	0.16	2,117 ± 279
Ultrasonic back fat, mm	1	0.38	0.03	0.05	0.10	1.48 ± 0.14
HGP back fat, mm	1	0.38	0.03	0.03	0.03	2.53 ± 0.38
HGP muscle depth, mm	1	0.24	0.02	0.02	0.03	7.21 ± 0.56
Feed intake, g/d	1	0.19	0.03	0.20	0.27	13,324 ± 1,647
	2	0.35	0.03	0.17	0.25	24,568 ± 6,326
Residual feed intake, g/d	1	0.11	0.04	0.21	0.25	3,883 ± 723

[1] Model 1: Animal model without social effects, Model 2: Animal model including heritable social effects.
[2] Heritability (h^2) was replaced by the proportion of the heritable variance compared to phenotypic variance (T^2) and the additive genetic variance (σ^2_A) was replaced by the σ^2_{TBV} when Model 2 was used. See Bijma et al. (2007a and 2007b) for derivation of formulas. Pen size (n) of 8.5 and average relatedness within pens (r) of 0.18 was used;
[3] based on live weight;
[4] based on hot carcass weight (used to estimate live weight).

Therefore, they were reported twice, once applying a model *without* a social genetic effect (Model 1) and once *with* a social genetic effect (Model 2). The most pronounced genetic correlations were those between daily gain and feed intake. The correlations between them were high, not only for the direct animal effect but also for social effects. The genetic correlation between backfat thickness and residual feed intake was also high (r_g=-0.54; p<0.05).

Table 6.4 Heritability (h^2), repeatability (r^2) and additive genetic variance (σ^2_A) estimates for lactation performance traits.

	h^2	r^2	σ^2_A
Weight at start, kg	0.50	0.57	134.9 ± 25.2
Fat mass at start, kg	0.42	0.58	21.7 ± 4.5
Weight loss during lactation, kg	0.14	0.19	19.6 ± 6.9
Lactation feed intake, kg	0.23	0.30	62.7 ± 13.6
Litter weight gain, kg	0.16	0.25	17.2 ± 5.3
Lactation efficiency, %	0.10	0.19	11.2 ± 5.6

Table 6.5 Genetic correlations among growing-finishing traits[1].

		Daily gain		Ultrasonic back fat	HGP muscle depth	Feed intake	Feed intake		Residual feed intake
		Direct	Social				Direct	Social	
Daily gain, g/d		-	-	0.00	-0.06	**0.82**	-	-	0.11
Daily gain, g/d	Direct		0.01	0.02	-0.08	-	**0.80**	-0.13	0.10
	Social			**-0.34**	-0.08	-	-0.22	**0.72**	-0.01
Ultrasonic back fat, mm					**-0.11**	**0.32**	**0.32**	-0.22	**-0.54**
HGP muscle depth, mm						-0.18	-0.18	-0.35	-0.18
Feed intake, g/d							-	-	**0.34**
Feed intake, g/d	Direct							0.05	**0.36**
	Social								0.31

[1] Correlations in bold did differ significantly from zero (p<0.05).

Genetic correlations among lactation performance traits

High litter weight gain and milk yield are genetically associated with a high feed intake capacity of lactating sow (Table 6.6). High feed intake capacity was associated with a low feed efficiency. This was valid for grower-finishers as well as for lactating sows. Sows that were heavier at start of lactation showed a higher fat mass (r_g=+0.61) and a reduced weight loss during lactation. The consequences of or the reasons for the reduced weight loss during lactation are not clear: feed intake was unaffected, litter weight gain might have been decreased and lactation efficiency might have been increased. However, none of these genetic correlations were significantly different from zero.

Genetic correlations between lactation performance traits and growing finishing traits

Contrary to the genetic correlations with the direct genetic effects, none of the genetic correlations of lactation performance traits with either one of the social genetic effects were significant (Table 6.7). High standard errors of the social genetic effects, expressed as percentage of the estimates, compared to the direct genetic effects can be an explanation.

The genetic correlation between backfat thickness during the finishing phase and fat mass at start of lactation was high. The genetic correlation of all other growing-finishing traits and fat mass at start of lactation pointed in the same direction as

Table 6.6 Genetic correlations among lactation performance traits[1].

	Fat mass at start	Weight loss during lactation	Lactation feed intake	Litter weight gain	Lactation efficiency
Weight at start, kg	**0.61**	**-0.36**	0.07	-0.14	0.19
Fat mass at start, kg		-0.17	-0.05	-0.21	0.05
Weight loss during lactation, kg			-0.41	0.22	0.25
Lactation feed intake, kg				**0.58**	**-0.64**
Litter weight gain, kg					-0.33

[1] Correlations in bold did differ significantly from zero (p<0.05).

Table 6.7 Genetic correlations between lactation performance traits and growing-finishing traits[1].

Growing-finishing traits	Lactation performance traits	Weight at start	Fat mass at start	Weight loss during lactation	Lactation feed intake	Litter weight gain	Lactation efficiency
Daily gain, g/d		**0.24**	0.05	-0.15	**0.29**	0.13	-0.13
Daily gain, g/d	Direct	**0.27**	0.05	-0.17	**0.30**	0.13	-0.07
	Social	-0.13	-0.32	-0.13	0.15	-0.09	0.27
Ultrasonic back fat, mm		-0.03	**0.53**	**-0.42**	-0.06	**-0.27**	-0.06
HGP muscle depth, mm		-0.14	**-0.18**	0.15	-0.10	-0.08	-0.15
Feed intake, g/d		0.13	**0.21**	-0.24	**0.23**	0.00	-0.33
Feed intake, g/d	Direct	0.12	**0.22**	-0.29	**0.24**	0.02	-0.32
	Social	-0.11	0.09	-0.35	0.06	0.28	0.11
Residual feed intake, g/d		-0.06	**-0.35**	0.32	0.18	0.18	**-0.51**

[1] Correlations in bold did differ significantly from zero (p<0.05).

the genetic correlation of these growing-finishing traits with backfat thickness. This supports the finding that backfat thickness as a grower-finisher is to a high extent, the same trait as fat mass at start of lactation as a sow. Backfat thickness as a grower-finisher was also associated with weight loss and litter weight gain during lactation. The latter traits did not show a significant genetic correlation with fat mass at start of lactation, although the genetic correlations point in the same direction. Higher daily gain as a grower-finisher was associated with higher weight at start of lactation. Sows with higher daily gain are expected to have higher feed intake during lactation. Feed intake as a grower-finisher had a small, but significant, genetic correlation with feed intake as a lactating sow. Next to the genetic correlation between ultrasonic back fat thickness and fat mass, the genetic correlation between residual feed intake as a grower-finisher and lactation efficiency as a sow was the most pronounced genetic correlation found.

6.4 DISCUSSION

Heritabilities

The estimates of heritabilities for growing-finishing traits, using a model without heritable social effects (Model 1) were remarkably similar to those previously reported by Bergsma et al. (2008a). Adding a fixed effect of compartment and a random effect of compartment within contemporary group hardly affected those estimates. The variance due to the effect of compartment within contemporary group (f^2) was rather large, especially for daily gain and feed intake as it was 17% and 27% of the phenotypic variance, respectively (Table 6.3). The variance explained by the effect of compartment within contemporary group in this study was apparently assigned to the group effect in the previous study. The variances due to the group effect and the effect of the compartment within contemporary group add up to the variance due to group effect alone of the previous study.

The proportions of the heritable variance compared to the phenotypic variance (T^2) for daily gain and feed intake, in case heritable social effects were included (Model 2), were substantially lower than those previously reported by Bergsma et al. (2008a). Compared to the statistical models in that study, in the present study two effects were added: (1) a fixed effect of compartment; and (2) a random effect of compartment within contemporary group. Apparently, compartment and additive social effects were (at least partly) confounded, which caused overestimation of the social effects in the previous study. Genetic correlations between the direct and social effect were almost zero (Table 6.5), while the genetic correlations in the

previous study were positive. A reduced covariance was the second reason why the T^2 estimates in the present study were lower than in the previous one since the covariance is part of the total animal variance (σ^2_{TBV}). Besides a change in the statistical model, the number of observations was almost doubled in the present dataset compared to the previous study. Although the T^2 estimates were substantially lower than in the previous study, heritable variance in growth rate was still about 50% and in feed intake even about 100% greater than suggested by classical heritability.

Heritabilities for lactation performance traits given in Table 6.4 are in line with those found by Bergsma et al. (2008b), which was expected since datasets from both studies overlapped considerably. The highly negative genetic correlation between backfat thickness and residual feed intake (r_g=-0.54; Table 6.5) might have been caused by an overestimation of the energy used for lipid deposition.

The consequences of including social effects

Taking heritable social effects into account for daily gain and feed intake did not affect the genetic correlation estimates. There were only minor differences between genetic correlations with the direct genetic effect of Model 2 compared to genetic correlations with the animal effect of Model 1, within the same trait (Table 6.5 and Table 6.7).

The direct animal effect and the social animal effect are genetically uncorrelated for daily gain and feed intake (r_g=0.01 and 0.05 respectively). The group effect and effect of compartment within contemporary group are non heritable social effects. Both their estimated variance, relative to the phenotypic variance (g^2 and f^2) was higher using Model 1 compared to Model 2. The true heritable social effect estimated using Model 2 might be included in the non heritable effect when Model 1 was used. In case heritable social effects can be mistaken for heritable direct effects in a model without accounting for heritable social effects (Model 1), genetic correlation estimates for the present trait with other traits, might be affected. This can, for example, happen in case of a positive genetic correlation between the social and direct effect when penning littermates. The social effect of the littermates will be mistaken for a direct effect of the animal itself. In our situation the genetic correlation between the social and direct effect for feed intake and daily gain is close to zero. Besides, social effects seem to be part of the random group- or compartment within contemporary group-effect in a model without accounting for heritable social effects (Model 1). Therefore it plausible that genetic correlation estimates are unaffected while excluding (Model 1) or including (Model 2) a heritable social effect in the model.

Animals with a high breeding value for the social effect on daily gain, will have less ultrasonic backfat themselves (r_g=-0.34; $p<0.05$). This might have been the consequence of a reduced appetite since the genetic correlation of the social effect on daily gain with the direct effect of feed intake was -0.22, although it was not significant statistically. A high social effect on daily gain was associated with a high social effect on feed intake (r_g=0.72). There was apparently no genetic association of daily gain with feed efficiency (neither of the direct nor the social effect). The expectation, raised in the introduction, that animals in 'high-social' pens spend less energy on fighting and stress, and thus become more efficient, could not be confirmed. A social effect on daily gain exists regardless of feeding strategy (*ad lib* or restricted) (Bergsma et al., 2008a). If animals with a high breeding value for the social effect on daily gain ate less themselves (and became leaner) more feed was left over and pen mates were able to express a higher feed intake and thus a higher daily gain, especially if the amount of feed on pen level was restricted. This phenomenon explains why a social effect was found for both *ad lib* and restricted fed animals.

Genetic correlations between lactation performance and growing-finishing traits

Development of an animal is a process that starts at fertilization and ends at maturity. Different growth phases are auto correlated because of underlying development processes. The growth curve of an animal is assumed to be a function of the adult weight of that animal. Gompertz-curves, for example, are often used to describe the growth of the pig. A Gompertz-curve uses three genotype parameters: mature body protein mass, mature body lipid mass, and the rate parameter of the Gompertz curves that potential body protein growth and desired body lipid growth are presumed to follow (Knap, 2000). Given this, the positive genetic correlations between daily gain as a grower-finisher and starting weight as a lactating sow (r_g=0.24) and especially between off test back fat and fat mass as a lactating sow (r_g=0.53) can be expected.

From the onset of parturition, genetic regulation of feed intake during lactation seems to differ from the genetic regulation of feed intake during growing-finishing since there is only a small positive, genetic correlation between them, whereas feed efficiency showed a higher similarity between lactation and growing-finishing, given the genetic correlation of -0.51 between lactation efficiency and residual feed intake during growing-finishing. A high residual feed intake means that animals are not very efficient, and therefore a negative correlation is expected.

Animals with a high genetic merit for feed intake during growing-finishing had a higher fat mass at start of lactation (r_g=+0.21). The genetic correlation between daily gain during growing-finishing and feed intake during lactation was even higher (r_g=+0.29) than the genetic correlation between feed intake as a grower-finisher and feed intake as a lactating sow (r_g=+0.23). This could be due to the effect of a large body size on the capacity to eat large amounts of feed.

Fat genotypes at start of lactation or as a grower-finisher tended to loose less weight during lactation (r_g fat mass and weight loss = -0.17; r_g back fat and weight loss = -0.42) compared to leaner genotypes. Whittemore and Morgan (1990) suggested that lean genotypes of sows may be less likely to mobilize fat stores than fatter genotypes. Our results appear to falsify this self protecting mechanism. We demonstrated that selection for feed intake during growing-finishing increases fat mass at start of lactation (r_g=+0.21). There is a negative phenotypic relation between fatness of the sow at start of lactation and feed intake during lactation. This phenomenon can have influenced our estimates since there is no measure of fatness included in the model for feed intake during lactation. Including fat mass as such, however, did not affect our genetic correlation estimate (results not shown).

Rauw et al. (2009) conducted a selection experiment in mice to investigate the relationship between food intake during growth and lactation food intake. They did not find a straightforward correlation either. They concluded that the relationship between food intake during growth and during lactation may have been reflected in the relationship between growth intake and body condition.

Feed intake during finishing and during lactation

The control of feed intake and regulation of energy use are extremely complex and are influenced by a large number of factors. Voluntary feed intake is regulated at two levels (Revell and Williams, 1993). The first is short-term regulation, which involves the factors regulating meal eating behavior, i.e. meal size and meal length. The second is a long-term regulation, which determines the average daily intake over a period of time. Signals from the gastrointestinal tract are likely to be of major importance in the short-term control of voluntary feed intake. Metabolic factors are likely to be more important for long-term control.

The physiological drive of lactating sows to produce milk at the expense of other body functions is a key component of the metabolic state of lactating sows. Therefore, it is likely that milk production is an important drive to consume feed. Milk production on its turn is primarily affected by the nursing demand of the suckling pigs during lactation (King, 2000). Given this, the control of feed intake as a lactating sow is different from that of a grower-finisher. This might explain the

relatively low genetic correlation for feed intake with feed intake as a grower-finisher.

Cameron et al. (2002) compared lactation performance in Large White gilts between lines that had been divergently selected for daily food intake during growing-finishing. Lactation food intake did not differ significantly between these selection lines, nor did live weight. Selection for high daily food intake of grower-finishers resulted in higher back fat thickness at start of lactation. The results of Cameron et al. (2002) were in line with our results. The only exception was the genetic correlation of feed intake as a grower-finisher and feed intake during lactation which was, although small, positive in our study.

Our estimates of genetic correlations are primarily based on mother-offspring comparison. The mothers were from dam lines or from commercial crosses of dam lines. Selection pressure in these lines is predominantly on fertility traits. Information on sire lines hardly contributed to the genetic correlations, since no information on lactation traits was available for these lines. Therefore, these estimates of genetic correlations were based on a population with only mild selection pressure on growing-finishing traits.

At Iowa State University, differences between generation 6 of a line selected for low residual feed intake and a control line were analyzed (Young et al., 2010). It was concluded that selection for low residual feed intake as a grower-finisher significantly reduces feed intake as a lactating sow. In our study, the genetic correlation between residual feed intake as a grower-finisher and feed intake as a lactating sow was, although positive, not significantly different from zero. Genetic correlations can change over time as a consequence of selection. This might explain the differences found in both studies. No direct selection on residual feed intake took place in our population, while the Iowa State-population was selected for residual feed intake only for at least 6 generations. Probably some indirect selection on lactation efficiency was performed in the dam lines of our study since the average lactation efficiency in our dataset was much higher compared to the Iowa State dataset (71% compared to about 36%, applying the same definition). The reduction of feed intake in lactating sows in the Iowa State experiment suggests that there is a positive genetic correlation between feed intake as a grower-finisher and as a lactating sow, since the correlation between residual feed intake and feed intake as a grower-finisher is positive (r_g=+0.34 and +0.36 in our study, applying Model 1 and 2 respectively).

There are moderate to strong (negative) phenotypic and genetic correlations between feed intake during lactation and weight and fat losses during lactation (Bergsma et al., 2008b). Culling decisions of farm managers on breeding farms on

sows after weaning are probably affected by feed intake since severe body mobilization (thin sows!) is expected to negatively affect the performance in the next production cycle. This raises the expectation that there is a continuous selection on feed intake during lactation.

In the introduction we raised the expectation of a moderately positive genetic correlation between feed intake as a grower-finisher and as a lactating sow. In this study we found at the most a small positive genetic correlation. On the other hand, feed efficiency as a grower-finisher and as a lactating sow showed a rather high genetic correlation. Body condition at start of lactation and the milk production stimulant by piglets were probably the cause of the unexpected low genetic correlation between the feed intake traits.

Selection for growing-finishing characteristics in the investigated dam line populations is not an immediate risk for lactation performance characteristics. Severe (unilateral) selection on feed efficiency during growing-finishing might negatively affect feed intake during lactation on the long run. This study provides the genetic parameters to quantify the consequences of and to optimize selection for growing-finishing traits and lactation performance traits in dam lines.

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Appendix

$Caculated\ live\ weight, kg =$

$1.3 \times Hot\ Carcass\ Weight, kg - 0.0025 \times Hot\ Carcass\ Weight, kg^2 + 0.2075 \times Hot\ Carcass\ Weight, kg$

(Handboek varkenshouderij, 2004)

Formulas used for the estimation of residual feed intake.

$\%fat = \dfrac{Ultrasonic\ Back\ Fat, mm - 1.87}{53.3}$ Default: 0.10

$\%protein = 0.165 - \left[0.00025 \times \left(\dfrac{On\ Test\ Weight, kg + Off\ Test\ Weight, kg}{2} - 80\right)\right]$

$Maintenance, J/d = \dfrac{(Off\ Test\ Weight, kg^{1.75} - On\ Test\ Weight, kg^{1.75}) \times 420}{(Off\ Test\ Weight, kg - On\ Test\ Weight, kg) \times 1.75}$

(De Haer, 1993)

$Water\text{-}protein\text{-}ratio = 5.39 \times \left(\%protein \times \dfrac{On\ Test\ Weight, kg + Off\ Test\ Weight, kg}{2}\right)^{-0.145}$

(De Greef, 1994)

$Lipid\ deposition, g/d = \dfrac{(Off\ Test\ Weight, kg \times 0.95 \times \%fat\text{-}of f test - On\ Test\ Weight, kg \times 0.95 \times \%fat\text{-}ontest) \times 1000}{Test\ Length, d}$

$Protein\ deposition, g/d = \dfrac{Daily\ Gain, g/d - Lipid\ Deposition, g/d}{Water\text{-}protein\text{-}ratio + 1}$

$Residual\ Feed\ Intake, g/d = \dfrac{Feed\ Intake, g/d \times 13.5 - Maintenance, J/d - (Protein\ Deposition, g/d + Lipid\ Deposition, g/d) \times 53}{13.5}$

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Breeding for reduced thermal sensitivity of feed intake in the lactating sow

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Abstract

The aims of this study were firstly, to evaluate the effects of climatic parameters on daily feed intake of lactating sows and secondly, to establish whether the response of sows to variation in temperature on feed intake during lactation was heritable. A total of 82,614 records for daily feed intake during lactation were available for 848 sows with 3,369 litters farrowing from January 2000 to December 2007. Climatic parameters were available from the nearest weather station, including maximum outside temperature, day length changes and humidity. Although ambient room temperature was modified at the animal level in the farrowing shed, these climatic parameters still had a significant effect on feed intake during lactation. Regression coefficients for temperature (T) and humidity (H) were $0.01385T-0.00031T^2$ and $0.01443H-0.00009H^2$. There was an interaction between T and H, partly due to the climate control in the farrowing shed. At low T, feed intake increased considerably with higher H in contrast to a small reduction in feed intake for high H at high T. Day length change was modeled with a cosine function. At start of autumn (September 21) sows ate 0.36 kg/d less feed then at start of spring (March 21). Daily feed intake during lactation was described as a function of days in lactation and as a function of both days in lactation and maximum 24 hour outside temperature of the nearest weather station using random regression models. The average heritability and repeatability summarized over the day in lactation at the mean temperature were 0.21 and 0.69 respectively. Genetic variance of temperature response on feed intake was less than 20% of the day effect. The permanent environmental variance was twofold (day) and fourfold (T) higher than the corresponding additive genetic variance. Heritabilities of daily feed intake were higher during the first week of lactation compared to the rest of lactation. The genetic correlation between days decreased as time increased down to about 0.2 between the first and last day in lactation. The genetic correlation between the temperature effects on feed intake remained positive within one standard deviation (+/-) of the temperature. The genetic correlation between feed intake records at the extreme temperatures decreased to about -0.35. It was concluded that random regression models are useful for research and results may be used to develop simpler models that can be implemented in practical breeding programs. An effect of temperature on lactation feed intake was found even in this climate-controlled environment located in a temperate climate zone. Larger effects are expected in more extreme climatic conditions with less temperature-controlled farrowing sheds.

Key words: Lactation, Random regression, Sow feed intake, Temperature tolerance

7.1 Introduction

Commercial pig breeding is a global industry. Therefore, it is important to know whether pigs are able to perform in a wide variety of environments that differ in regard to potential stressors. Pig genotypes may differ in their response to changes in the prevailing environment giving rise to a genotype by environment interaction. Calculations have shown that in the presence of a genotype by environment interaction the selection for high productivity in a non-limiting environment resulted in an increased environmental sensitivity (Kolmodin et al. 2003). For reproductive performance, Bloemhof et al. (2008) found a significant difference in heat tolerance between two purebred dam lines. One of the lines was a high productive line, raised in nucleus herds with superior environments in a temperate environment. The other dam line was a less productive line predominantly raised in tropical environments.

Sometimes environmental conditions may be described on a continuous scale using a range of descriptors such as temperature or change in day length which quantifies climatic and seasonal influences. In these situations, reaction norm models are useful tools for genetic analysis (de Jong, 1995). These models express performance of a genotype as a function of the environment thereby providing avenues for selection of highly productive animals with low environmental sensitivity.

Lactation is a critical phase for piglets as well as for sows. A high and undisturbed lactation feed intake of the sow ensures a good start of life of piglets and good prospects for the sow for ongoing reproductive success in future parities. However, undisturbed feed intake during lactation is not always achieved. For example, high temperatures have been shown to reduce feed intake in lactating sows (i.e. Black et al., 1993; Quiniou and Noblet, 1999). The effect of temperature has to be separated from other climatic and seasonal factors such as humidity and day length, in order to quantify the specific response of each genotype to changes in temperature and other climatic factors influencing feed intake of lactating sows. Therefore, the aims of this study were a) to evaluate the effects of climatic parameters on daily feed intake of lactating sows and b) to establish whether the response of feed intake of sows during lactation to variation in temperature was heritable.

7.2 Material and methods

Animals were subjected to standard production conditions and no additional measurements were taken. Consequently no approval of the Care and Use Committee approval was needed. The experimental farm of the Institute of Pig Genetics (IPG), where all observations originated from, is operating in line with the regulations of the Dutch law on protection of animals.

Dataset

The experimental farm of IPG in Beilen (52° 52' Lat. 06° 31' Lon., The Netherlands) is used to compare commercial TOPIGS crossbred sows (Vught, The Netherlands) and their offspring based on inseminations with boars from different commercial sire lines. In total, 82,614 daily feed intake observations during lactation were available for 848 sows from 7 line crosses with 3,369 litters, recorded from January 2000 until December 2007. The pedigree file was based on three generations of parents and contained 2,963 animals. Observations on feed intake were available for 780 sows with known parentage (loosing 68 sows due to lack of pedigree) which descended from 110 sires and 410 dams.

Climatic data and climate control on farm

Daily temperature (mean, minimum, maximum) and humidity (daily mean relative atmospheric humidity) were available from the nearest weather station in Eelde (53° 08' Lat. 06° 35' Lon.) 30 km away from the experimental farm of IPG in Beilen (KNMI, 2010). Day length on June 21 and December 21 was 16 hours 53 minutes and 7 hours 36 minutes, respectively. Day light was admitted to each farrowing room via windows. Artificial light was only switched on during animal handling. Heat lamps were used only for the first 72 hours post farrowing. From July 2004 onwards, ambient room temperature of each farrowing room as well as the outside temperature were recorded each hour at the experimental farm.

Farrowing rooms were ventilated mechanically with inlet air entering the farrowing room via a central corridor where heating elements were located. It was not possible to apply air cooling. At the day of parturition the target value for the ambient room temperature was 26°C, which was gradually reduced to the target value of 25°C until day 18 after farrowing. The desired farrowing room temperature was adjusted to the piglets' requirements to prevent cold stress.

A three-week batch farrowing system is used at the IPG-farm consisting of 24 sows which farrow in three farrowing rooms (with eight farrowing crates each). The sow that farrows first in a farrowing room determines the temperature regime in that

farrowing room. The average interval between first and last parturition date was 5.3 days within each farrowing group.

Feeding schemes

Sows were transferred to the farrowing house on average 8.8 days before parturition. Sows were gradually adapted to a lactation diet, which was fed restrictively applying separate feeding schemes for primiparous and multiparous sows. The feeding scheme represented the maximum amount of feed offered to the sow by a computerized feeding machine. Once a day the farm manager decided if the amount of feed allocated to a sow needed to be reduced to avoid losses. The daily feed allowance was based upon the feed intake capacity of the sow and was not affected by the sow's weight, her condition or the number of piglets to be nursed. The feed intake capacity of the sow was determined as the amount of feed not eaten by the sow two hours after delivery of feed. The amount of feed was reduced if a sow was unable to eat the entire meal. Sows were fed twice a day at approximately 0700 h and 1500 h.

On average piglets were weaned at 27.3 days of age. Only the first 28 days of lactation were included in the analyses, because the number of observations decreased rapidly after day 28 of lactation. Feed intake records at the day of parturition (defined as day zero) and at the day of weaning of the piglets were excluded.

Net energy content of the commercial lactation diet used at the IPG farm was 9.68 MJ NE per kg feed, which corresponds to 13.5 MJ ME per kg feed. The pelleted feed supplied contained 147.2 g of crude protein and 8.1 g of lysine per kg feed.

Statistical analysis

Fixed effect model selection

Using inside or outside temperature observations or both, one can define an almost infinite number of temperature characteristics such as the maximum or the minimum daily temperature, the largest difference in daily temperature and use these characteristics recorded on the day of feed intake or on any day shortly before the actual day of feeding. Likewise, deviation from desired ambient room temperature can be based on numerous different temperature characteristics. In a preliminary study, the maximum 24-hour temperature on the day of feed intake appeared to explain most of the variation in feed intake in comparison to other possible choices for temperature (results not shown). In addition to the temperature measurement, the type of temperature measurement must be selected: ambient room temperature, outside temperature (on farm or weather

station) or deviation from the desired ambient room temperature. In that same preliminary study, the coefficients of determination of the models to explain variation in daily feed intake containing different temperature measurements were almost identical (results not shown). Therefore, maximum 24-hour temperature of the nearest weather station was used further on in this study since inside ambient room temperature measured on farm was only available for a subset of sows. In addition, a high accuracy of measurements can be achieved at weather stations because the equipment is well maintained and regularly calibrated.

PROC MIXED (SAS, 1999) was used to determine the fixed effect model which fitted daily feed intake during lactation best (Model 1):

$$DFI_{ijklmn} = \mu + DAY_i(FEEDSCHEME_j) + PARITY_k + LINE_l + b_1TOBN + b_2DL + b_3DLC + b_4HM + b_5HM^2 + b_6T + b_7T^2 + \underline{BATCH_m} + \underline{SOW_n} + e_{ijklmn}$$

where:

DFI_{ijklmn}=Daily feed intake (kg/d) of sow n;

DAY_i =the effect of day i during lactation (i=1 to 28);

$FEEDSCHEME_j$= the effect of feeding scheme j (j=0,1) for primiparous versus multiparous sows;

$PARITY_k$=the effect of parity k of multiparous sow n combining parity six and higher (k=1 to 6);

$Line_l$= the effect of genetic line (=commercial cross) l of sow n (l=1 to 7);

TOBN=Number of piglets to be nursed;

DL= Day length parameter (for explanation see section 'day length function' below);

DLC= Day length-change parameter (for explanation see section 'day length function' below); HM=relative atmospheric humidity (%);

T=Maximum 24 hour outside temperature reported by the nearest weather station;

$BATCH_m$=the (random) effect of the mth three-week contemporary group based on date farrowing m=1 to 156);

SOW_n=the (random) effect of the nth sow (n=1 to 848);

e_{ijklmn} is the residual effect of sow n in her k^{th} parity belonging to line l on day i of lactation applying feeding scheme j within batch m; b_1 up to b_7 are coefficients of linear regression on their independent effects.

Number of piglets to be nursed was part of the model because, according to Revell and Williams (1993) it is likely that milk production is an important drive to consume feed. The number of piglets to be nursed affect milk yield of sows.

Day length function

Day length and temperature are at least partly confounded. Day length can be modeled by taking the (trigonometric function) sine of the day (1 to 365) of feed intake within a year, making sure that the peak of the curve is at start of summer (June 21). Or as a formula:

Day length = sin(((DateFeedIntake -'21MAR1999')/365.25)*(2π))

The first derivative of day length gives the changes in day length at the day of feed intake (further on called 'day length change'), which is the cosine of the day length function. The amount of change in the day length is largest at start of spring and autumn with function values of 1.0, increase in day length, for the 21st of March and -1.0, decrease in day length, for the 21st of September (Figure 7.1).

Development of random regression models

The mean feed intake curve derived from the fixed effects outlined in Model 1 was fitted for primiparous and multiparous sows and deviations in daily feed intake from this curve were estimated for batch, additive genetic and permanent environmental effect of the sow. Sensitivity of sows to temperature was modeled by applying a reaction norm for each animal, representing its EBV for feed intake, on values of temperature on the day of feed intake.

Models were progressively extended to higher order Legendre polynomials for feed intake on days of lactation (Model 2) as well as feed intake on different temperatures on the day of feed intake (Model 3).
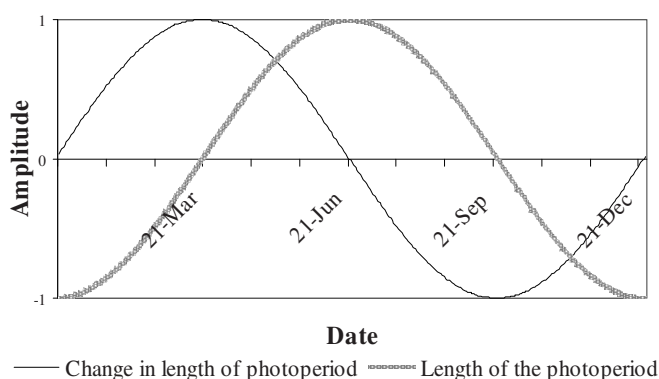
Figure 7.1 Progression of the length of the day over the year and its first derivative which describes the amount of change in the length of the day over the year.

Several types of orthogonal polynomials are available, but Legendre polynomials have been commonly used in genetic evaluation of repeated records on individuals over time and in analysis of genotype by environment interaction (Schaeffer, 2004). Analyses were performed using ASREML software (Gilmour et al., 2006). To estimate variance components without including sensitivity to temperature the general mixed model was applied:

$$DFI_{ino} = fixed +$$

$$\sum_{p=1}^{k_T} \beta_{np}\, \theta_p(T_{on}^*) + \sum_{q=0}^{k_{day}} \alpha_{nq}\, \phi_q(day_{in}) + \sum_{q=0}^{k_{day}} \delta_{nq}\, \phi_q(day_{in}) + \sum_{q=0}^{k_{day}} \gamma_{nq}\, \phi_q(day_{in})$$
$$+ \ \varepsilon_{ino}$$

To account for heritable temperature response of feed intake of sows during lactation, the subjoined was added to this general mixed model:

$$\sum_{p=1}^{k_T} \varphi_{np}\, \theta_p(T_{on}^*) + \sum_{p=1}^{k_T} \chi_{np}\, \theta_p(T_{on}^*)$$

where DFI_{ino} is the feed intake on day i (kg/d) of animal (sow) n at temperature o; *fixed* is the set of fixed effects as selected from Model 1; T_{on}^* is the standardized temperature class o at day of feed intake fitted as a fixed effect omitting an intercept. Temperature was transformed with mean=0 and STD=1, forming 55 classes with intervals of 0.1 STD (-2.5 to +2.9). Further, the fixed random regression coefficients for temperature to model the population mean are β_{np}; day_{in} is the day i of lactation at recording; α_{nq} and φ_{np} are the random regression coefficients for the additive genetic effects of animal n on day and temperature, respectively; δ_{nq} and χ_{np} are the random regression coefficients for permanent environmental effect of sow n on day and temperature, respectively; γ_{mq} are the random regression coefficients for animal's contemporary group (batch) for batch class m; $\theta_p(T_{on}^*)$ is the pth Legendre polynomial on temperature; $\phi_q(day_{in})$ is the qth Legendre polynomial of day i in lactation; k_{day} and k_T are the order of fit of the Legendre polynomials of day and temperature respectively and ε_{ino} is the random residual effect.

The log likelihood ratio test was used to compare the fit of two models with adjacent orders of polynomials. In matrix notation Model 2 and Model 3 were:

$$\mathbf{y} = \mathbf{X}\mathbf{f} + \mathbf{Z}_D \mathbf{a}_D + \mathbf{W}_D \mathbf{pe}_D + \mathbf{T}_D \mathbf{b}_D + \mathrm{e}$$

$$\mathbf{y} = \mathbf{X}\mathbf{f} + \mathbf{Z}_D \mathbf{a}_D + \mathbf{Z}_T \mathbf{a}_T + \mathbf{W}_D \mathbf{pe}_D + \mathbf{W}_T \mathbf{pe}_T + \mathbf{T}_D \mathbf{b}_D + \mathrm{e}$$

where **y** is the vector of observations; **f** is the vector of fixed effects selected from Model 1; **a** is the vector of random additive genetic effects; **pe** is the vector of random non-genetic effects of the permanent environmental effect of the sow; **b** is the vector of random effects common to sows with feed intake in the same batch; **X, Z, W** and **T** are incidence matrices and **e** is the vector of random residuals. The subscripts D and T represent day-dependent and temperature-dependent effects. The (co)variance matrix belonging to Model 2 was assumed to be:

$$
var\begin{bmatrix} \mathbf{a}_D \\ \mathbf{pe}_D \\ \mathbf{b}_D \\ \mathrm{e} \end{bmatrix} = \begin{bmatrix} \mathbf{K}_{a_D} \otimes \mathbf{A} & 0 & 0 & 0 \\ 0 & \mathbf{K}_{pe_D} \otimes \mathbf{I}_{pe_D} & 0 & 0 \\ 0 & 0 & \mathbf{K}_{b_D} \otimes \mathbf{I}_{b_D} & 0 \\ 0 & 0 & 0 & \mathbf{R} \end{bmatrix}
$$

and the (co)variance matrix belonging to Model 3 was:

$$
var\begin{bmatrix} \mathbf{a}_D \\ \mathbf{a}_T \\ \mathbf{pe}_D \\ \mathbf{pe}_T \\ \mathbf{b}_D \\ \mathrm{e} \end{bmatrix} = \begin{bmatrix} \mathbf{K}_{a_D} \otimes \mathbf{A} & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{K}_{a_T} \otimes \mathbf{A} & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{K}_{pe_D} \otimes \mathbf{I}_{pe_D} & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{K}_{pe_T} \otimes \mathbf{I}_{pe_T} & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{K}_{b_D} \otimes \mathbf{I}_{b_D} & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{R} \end{bmatrix}
$$

where $\mathbf{K}_{a_D}$, $\mathbf{K}_{a_T}$, $\mathbf{K}_{pe_D}$, $\mathbf{K}_{pe_T}$ and $\mathbf{K}_{b_D}$ are the matrices of coefficients of the covariance function for additive genetic, permanent environment of the sow and batch effects dependent on day (D) or temperature (T). Matrix **R** is a diagonal matrix containing residual variances depending on day of feed intake allowing heterogeneous residual variances. There were 19 measurement error categories since residual variances were allowed to differ for each day of the first 15 days of lactation. The residual variances were assumed to be constant for day 16-18, 19-21, 22-24, and 25-28 of lactation. The $\mathbf{I}_{pe_D}$, $\mathbf{I}_{pe_T}$ and $\mathbf{I}_{b_D}$ are identity matrices of the appropriate dimensions, and **A** is a matrix of additive genetic relationships among all individuals. The $\otimes$ indicates the Kronecker product of matrices.

The formula to calculate an overall genetic correlation between combinations of observations on two (different) days and two (different) temperature classes was:

$$r_{g_{1,2}} = \frac{cov(day_1, day_2) + cov(T_1^*, T_2^*)}{\sqrt{var(day_1) + var(T_1^*)} \times \sqrt{var(day_2) + var(T_2^*)}}$$

where day_i is the ith day in lactation; and T_o^* is the (transformed) temperature class o on day i.

The formula to calculate the heritability and repeatability of the average of n repeated records in a repeatability model was (extended from K. Meyer, Animal Genetics and Breeding Unit (AGBU), University of New England, Armidale, Australia, personal communication):

$$h^2 = \frac{\sigma_{a_D}^2 + \sigma_{a_T}^2}{\sigma_{a_D}^2 + \sigma_{a_T}^2 + \sigma_{pe_D}^2 + \sigma_{pe_T}^2 + \sigma_b^2 + \sigma_e^2/n}$$

$$r^2 = \frac{\sigma_{a_D}^2 + \sigma_{a_T}^2 + \sigma_{pe_D}^2 + \sigma_{pe_T}^2}{\sigma_{a_D}^2 + \sigma_{a_T}^2 + \sigma_{pe_D}^2 + \sigma_{pe_T}^2 + \sigma_b^2 + \sigma_e^2/n}$$

where $\sigma_{a_D}^2$ and $\sigma_{a_T}^2$ are the average additive variances over a trajectory of n observations for the day-dependent and temperature-dependent effect respectively; $\sigma_{pe_D}^2$ and $\sigma_{pe_T}^2$ are the average variances due to permanent environment for the day-dependent and temperature-dependent effect, respectively; σ_b^2 is the average variance due to the batch-effect, σ_e^2 is the average residual variance; and n is number of observations, here: the number of days in lactation.

7.3 Results

Data description

Descriptive statistics are given in Table 7.1 Outside temperature and humidity observations were available for the entire dataset. Observations on ambient room temperature were available on a subset of the dataset. The average outside temperature was 12.8°C whereas the average ambient room temperature was 25.2 °C. According to Black et al. (1993), the thermo-neutral zone for lactating sows lies

Table 7.1 Descriptive statistics for lactation feed intake as well as temperature and humidity characteristics.

	mean	stddev	min.	max.
Parity	3.5	2.1	1	12
Lactation length, d	27.3	4.5	14	28
Number of piglets to be nursed	12.1	2.6	6	20
Daily feed intake, kg/d	5.31	2.17	0	9.0
Daily mean outside temperature, ºC[1]	12.8	3.5	-9.6	25.5
Maximum outside temperature, ºC[1]	14.2	7.3	-4.1	35.4
Daily mean relative atmospheric humidity, %[1]	83.9	9.2	41	100
Daily mean room temperature, ºC[2]	25.2	1.4	17.9	30.3
Daily mean outside temperature, ºC[2]	11.4	6.3	-4.2	27.7
Maximum ambient room temperature, ºC[2]	26.1	1.8	18.4	36.0
Maximum outside temperature, ºC[2]	15.3	7.5	-2.6	34.5

[1] Weather station Eelde KNMI;
[2] On farm measurement; only available on a subset of the dataset (Number of sows=363; Number of litters=1,130; Number of days= 22,019).

between 12°C and 22°C. Consequently, sows are kept at ambient room temperatures that exceed the upper critical temperature. Note that heating was used to compensate for low temperatures but no air cooling could be applied. Consequently, at high outside temperatures, mechanic ventilation could not prevent ambient room temperature to rise. The tail of the temperature distribution to the right (higher temperatures) is therefore larger then the one to the left (lower temperatures).

Primiparous sows were fed a maximum of seven kg feed per day (Figure 7.2a) while the maximum feed allowance was eight kg per day for multiparous sows (Figure 7.2b). From day of parturition, sows were fed according to an ascending scale until they reached the maximum feed allowance at day 17 of lactation for primiparous sows and at day 13 of lactation for multiparous sows. Note that the average daily feed intake plus one times the standard deviation was in almost all cases higher than the feeding scheme. However, feeding sows a higher amount of feed than the feed allowance occurred only occasionally (less then 3% of daily feed intake records) indicating that the distribution of daily feed intake within a day was skewed with considerable variation in daily feed intake below the mean. The standard deviation increased as lactation increased until the plateau of the feeding scheme was reached after 14 days and remained relatively constant afterwards.
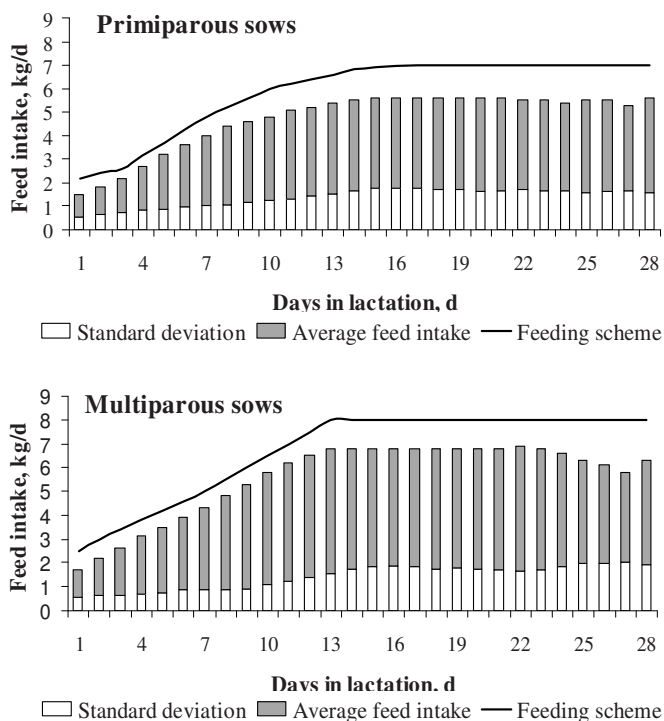
Figure 7.2a and 7.2b Daily feed allowances as defined by the feeding scheme, average realized feed intake per day and standard deviations of daily feed intake records for primiparous (7.2a) and multiparous sows (7.2b).

The relationship between daily feed intake during lactation and outside temperature is shown in Figure 7.3a and Figure 7.3b for primiparous and multiparous sows, respectively. There was no clear association between feed intake and outside temperature. The Netherlands has a maritime climate. The maximum outside temperature at the weather station nearest to the IPG-farm was 35.4°C and the lowest maximum outside temperature was -6.5°C over an eight-year period (Table 7.1). Extreme temperatures hardly happened and consequently the number of observations on days with extreme outside temperatures was limited (Figure 7.3a and Figure 7.3b).
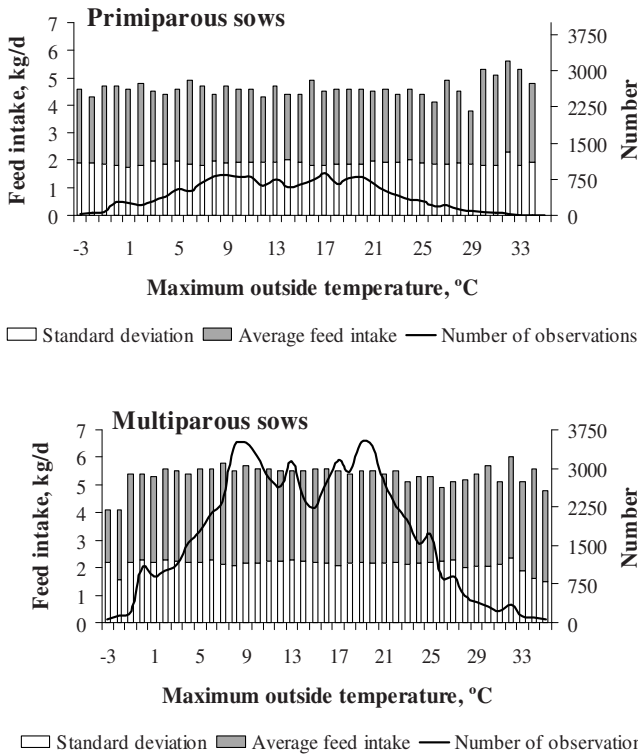
Figure 7.3a and 7.3b Realized daily feed intake, its standard deviation and number of observations of primiparous (7.3a) and multiparous sows (7.3b) related to maximum 24 hours outside temperature of the nearest weather station.

Phenotypic model
The results of the PROC MIXED procedure applying Model 1 are presented in Table 7.2 showing all significant effects. All effects of Model 1 were significant except day length.

Day length function
Day length change at the day of feed intake affected sows feed intake during lactation in contrast to day length which was not significant. Both functions were not exchangeable, since day length did not become significant when day length change was omitted from the model. The regression coefficient for day length change was: +0.18 (± 0.028), meaning that sows consumed 0.36 kg more feed per day at the start of spring compared to the start of autumn.

Table 7.2 Significance of model factors and variances explained by fixed and random effects applying Model 1 for daily feed intake. Only significant effects are shown.

Model factor	Variance	F-value	p-value
Day$_i$(Feedscheme$_j$)		2,264.44	<0.0001
Parity$_k$		55.41	<0.0001
Line$_l$		11.03	<0.0001
Piglets to be nursed		40.56	<0.0001
Day length change		41.79	<0.0001
Humidity (linear)		5.41	0.0200
Humidity (quadratic)		5.06	0.0244
Maximum outside temperature at weather station (linear)		21.30	<0.0001
Maximum outside temperature at weather station (quadratic)		11.15	0.0008
Variances explained by			
Total Fixed effects	2.7143		
Batch$_m$	0.0811		<0.0001
Sow$_n$	0.2690		<0.0001
Residual$_{ijklmn}$	1.7142		<0.0001
Total	4.7786		

Temperature and humidity

Both temperature (T) and humidity (H) were modeled applying a quadratic function. For temperature, the top of this function was at 22.4 °C. Sows ate 53 g/d feed less at the maximum of the maximum outside temperature which was 35.4 °C ($FI = 0.01385T\text{-}0.00031T^2$). For relative atmospheric humidity the top of the quadratic function was at 80 %. In comparison, feed intake was 145 g/d less at 40% relative atmospheric humidity and 37g/d and 35 g/d less at 60 and 100 % relative atmospheric humidity, respectively ($FI = 0.01443H\text{-}0.00009H^2$). Note that both thermal parameters were the temperature and humidity of the inlet air and thereby were not necessarily the temperature and humidity that sows experienced. The F-value of both the linear and quadratic term of relative humidity per se was relatively low. From a biological point of view this makes sense. Sows regulate their surface temperature by increasing or decreasing the blood flow subcutaneously. Therefore, sows lose most heat through non-evaporative heat loss (radiation, convection and conduction). Heat loss by respiration in pigs is low although pigs are able to dissipate heat by respiration (Curtis, 1983).

Different interactions were tested to obtain a better understanding of effects. Amongst them, the interaction between temperature and humidity was evaluated. If the interaction between maximum outside temperature and relative humidity

was included in the model, the F-value of temperature and humidity increased substantially. All five effects (humidity (linear); humidity (quadratic); maximum outside temperature at weather station (linear); maximum outside temperature at weather station (quadratic); and humidity (linear) by maximum outside temperature at weather station (linear)) became highly significant ($p<0.0001$) with no effect on the coefficient of determination of the full model. The decrease in daily feed intake with lower temperatures was more pronounced in combination with low humidity (Figure 7.4). For example, at a maximum 24-hour outside temperature of -6°C, daily feed intake was 0.88 kg higher at 100% humidity in comparison to a humidity of 40%. In contrast, at a high outside temperature of 34 °C daily feed intake actually increased with lower humidity levels. However, this interaction was mainly observed for low humidity levels at low temperatures which were represented by very few records given the mean and variation outlined in Table 7.1. In addition, the interaction did not improve the coefficient of determination and humidity was neglected further on in our random regression models to prevent over parameterization.
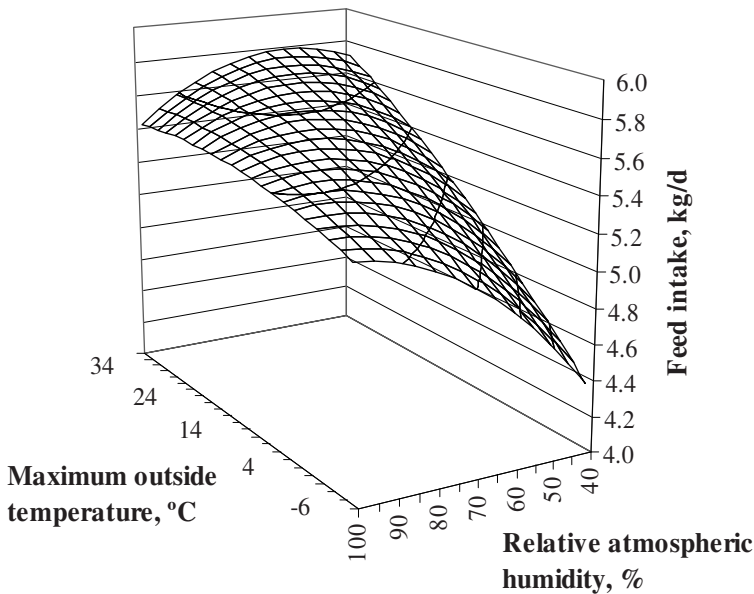
Figure 7.4 The effect of maximum outside temperature and relative atmospheric humidity measured at the nearest weather station on daily feed intake of sows during lactation.

Line crosses

The interaction between temperature and (genetic) line cross of the sow was investigated as well, which can be considered as the first step towards definition of a reaction norm for a specific genotype. Each line cross had its own reaction norm, which are shown for the four largest sow lines in Figure 7.5.

Feed intake in lactating sows was highest in the medium temperature ranges for three out of the four line crosses. Cross A and B responded similarly to temperature, although cross A had a higher feed intake. Cross D had a lower feed intake capacity and can not handle extreme temperatures as well as cross A and cross B. The difference between maximum feed intake at 17 °C and 36 °C was 0.22 kg/d for cross D. Cross C reacted differently. At temperatures below about 5 °C, sows of this cross responded by eating more. Cross C can be considered as the least temperature sensitive line, which has been investigated further by Bloemhof et al. (2008). To test whether or not there is a sow by temperature interaction, random regression techniques were applied.

Random regression

A number of tests were performed to evaluate the accuracy of random regression models. The mean feed intake curve derived from the fixed effects for primiparous
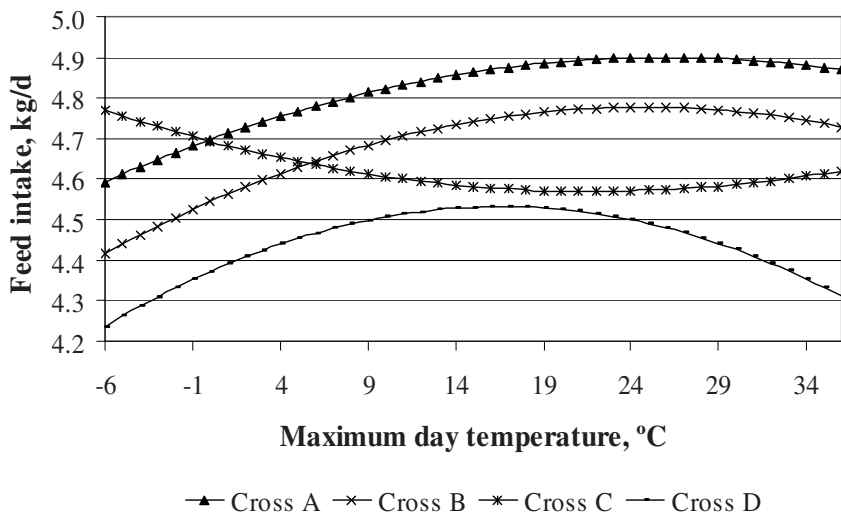
Figure 7.5 Reaction norms for line crosses of daily lactation feed intake records on maximum outside temperature measured at the nearest weather station.

and multiparous sows, applying Model 3, were similar to those depicted in Figure 7.2a and 7.2b. The solutions for the fixed effect of line cross, day length change, number of piglets to be nursed and parity of the sow were similar to those applying Model 1 (results not shown). The fixed effect of outside temperature was only small. The difference in feed intake at -4.1 °C compared to +35.4 °C was less than 0.3 kg/d. This might be expected given the lack of variation in mean feed intake observed across the temperature trajectory (Figure 7.3a and 7.3b). One of the reasons the results of Model 3 differ slightly from those of Model 1 is that we used a third order Legendre polynomial for the fixed effect of temperature applying Model 3, instead of a quadratic function applying Model 1.

Average variance components over both trajectories, 28 days of lactation (Model 2) and temperature (Model 3) are presented in Table 7.3 Variances (additive, permanent environment and total), heritability and repeatability per day of lactation are depicted in Figure 7.6a and 7.6b. A Likelihood ratio test showed that every extra order of the polynomial, starting at the first order, contributed significantly to a better fit of the data (p<0.001). A fifth order polynomial (q=5) for the random effects, applying Model 2, did not reach convergence and higher order polynomials were not tested.

The first four rows of Table 7.3 show that with increasing order of the polynomial, average heritability over the trajectory decreased. Average residual variance decreased whereas average additive animal variance remained more or less

Table 7.3 Variance components, heritability (h^2) and repeatability (r^2) for daily feed intake during lactation, averaged over 28 days, applying random regression models, excluding the additive animal effect of temperature response (Model 2) and including the additive animal effect of temperature response (Model 3).

Model	q	p	$\sigma^2_{A_D}$	$\sigma^2_{pe_D}$	σ^2_b	σ^2_e	$\sigma^2_{A_T}$	$\sigma^2_{pe_T}$	h^2	r^2
2	1	2	0.1672	0.2727	0.1258	1.7786	-	-	0.27	0.70
2	2	2	0.1747	0.2701	0.1538	1.7235	-	-	0.26	0.67
2	3	2	0.1719	0.2837	0.1976	1.6569	-	-	0.24	0.64
2	4	2	0.1624	0.3167	0.2087	1.6315	-	-	0.22	0.64
3	4	1	0.1477	0.3269	0.2091	1.6078	0.0052	0.0727	0.19	0.67
3	4	2	0.1487	0.3179	0.2103	1.5993	0.0187	0.1018	0.20	0.69
3	4	3	0.1546	0.3075	0.2096	1.5882	0.0274	0.1118	0.21	0.69

q and p are orders of fit for the Legendre polynomials for the day-effect and temperature effect, respectively; $\sigma^2_{A_D}$ and $\sigma^2_{A_T}$ are the average additive variances for the day-dependent and temperature-dependent effect; $\sigma^2_{pe_D}$ and $\sigma^2_{pe_T}$ are the average variances due to permanent environment for the day-dependent and temperature-dependent effect; σ^2_b is the average variance due to the batch-effect, σ^2_e is the average residual variance.
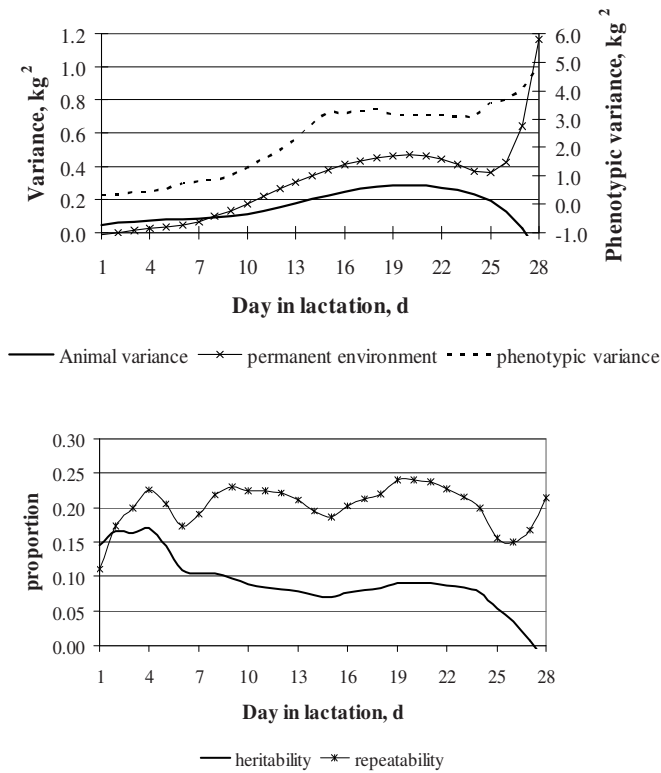
Figure 7.6a and 7.6b Variance components (7.6a) and ratios (7.6b) of daily feed intake during lactation depending on the day in lactation (Model 3).

constant. Average variance shifted towards permanent environment and batch effect. Additive variance over the trajectory increased with increasing day of lactation until maximum was reached at about three weeks in lactation (Figure 7.6a). After three weeks, additive variance decreased again. Total variance for each day in lactation $\left(\sigma_a^2 + \sigma_{pe}^2 + \sigma_b^2 + \sigma_e^2\right)$ followed the shape of the feeding scheme except for the last four days of lactation where the total variance increased rapidly. The latter effect was caused by an increased residual variance of the last error category (24-28 days). Heritability was highest during the first week of lactation and remained constant afterwards (Figure 7.6b). The drop in heritability from day 24 onwards was caused by an increase in residual variance during the last four days of lactation. In comparison, repeatability was rather constant over lactation.

Adding an additive genetic effect of temperature response on feed intake (Model 3) reduced the average additive variance of feed intake over days slightly (Table

7.3). With increasing order of the polynomial, the additive and permanent environment variance of temperature response in feed intake increased. Goodness of fit improved up to the third order polynomial (p=3) for the temperature dependent feed intake (likelihood ratio test: p< 0.001). The fourth order (p=4) did not reached convergence. At the third order polynomial, the additive variance of feed intake over temperature was less than 20% of the average additive variance of feed intake over days.

The average heritability was somewhat higher excluding an animal and permanent environment effect of temperature response on feed intake. The day-dependent as well as the temperature-dependent permanent environmental effect on daily feed intake was high. The day-dependent permanent environment variance was twofold higher than the day-dependent additive variance. The temperature-dependent permanent environmental variance was even fourfold higher than the corresponding additive variance. Sows have learned to modify feeding behaviors to cope with temperature and this impacts on the sows ability to express their genetic potential for lactation feed intake. The restricted feeding regime during lactation might have contributed to the limited expression of feed intake capacity during lactation.

The additive variance of temperature response in feed intake was more or less constant over the temperature trajectory (Figure 7.7), except for the extreme temperatures where genetic variance increased substantially. The permanent
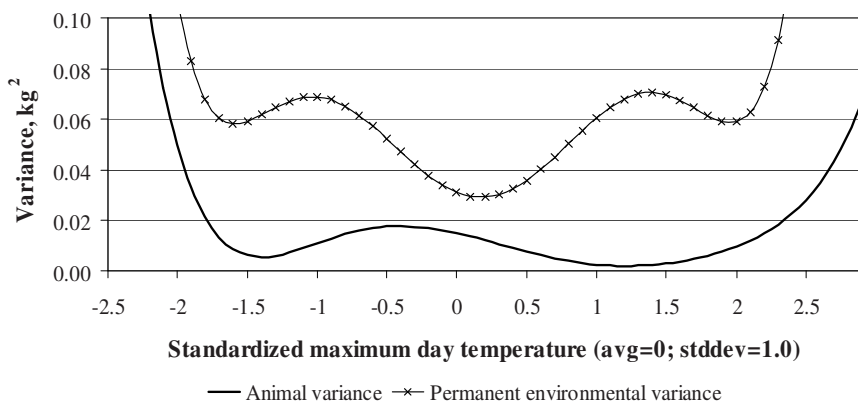
Figure 7.7 Additive and permanent environmental variance of daily feed intake during lactation depending on the maximum outside temperature measured at the nearest weather station (Model 3).

environmental variance of temperature response showed the same patterns as the additive variance of temperature response (Figure 7.7), in that respect that variances increased substantially at extreme temperatures.

Additive genetic covariance between days (Figure 7.8) and between temperature-classes (Figure 7.9) were also derived from the random regression models on daily lactation feed intake. Daily feed intake records which were approximately within seven days of each other were genetically the same trait with genetic correlations above 0.8 (Figure 7.8). As the time increased, the correlation between additive effects at different feed intake days was gradually reduced to 0.2 to 0.4 between the additive effects at the first and the last days of lactation. Whether temperature response on feed intake was excluded (Model 2) or included (Model 3) did not affect the course of the genetic correlations between feed intake at different days, since the upper triangle and lower triangle in Figure 7.8 are almost identical.

In the lower triangle of Figure 7.9 the overall genetic correlations at a fixed day in lactation (day 21) over the temperature trajectory, are presented. The lower
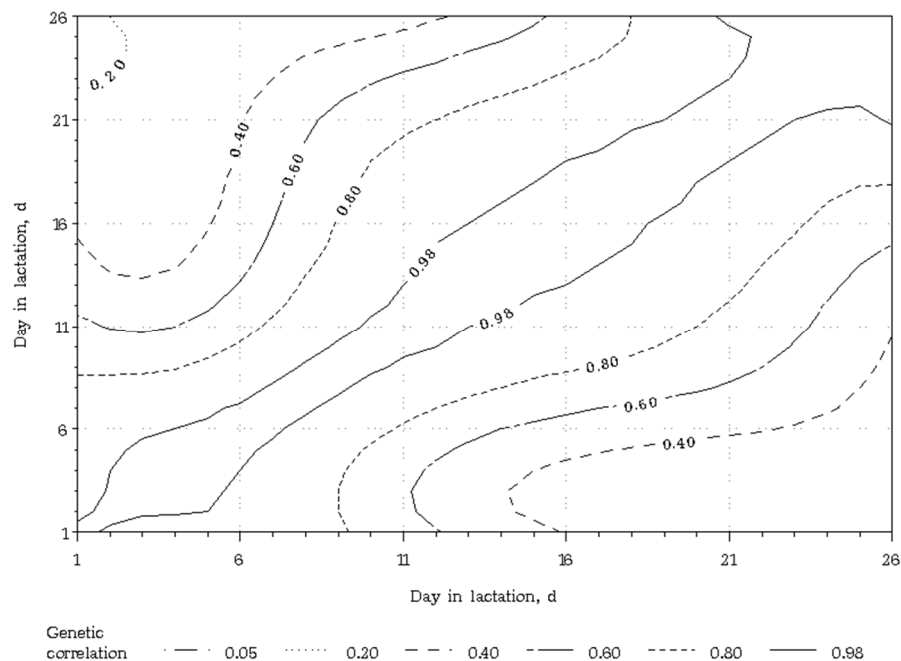
Figure 7.8 Genetic correlations between daily feed intakes at different days in lactation. Below the diagonal excluding temperature response (Model 2), above the diagonal including temperature response (Model 3).
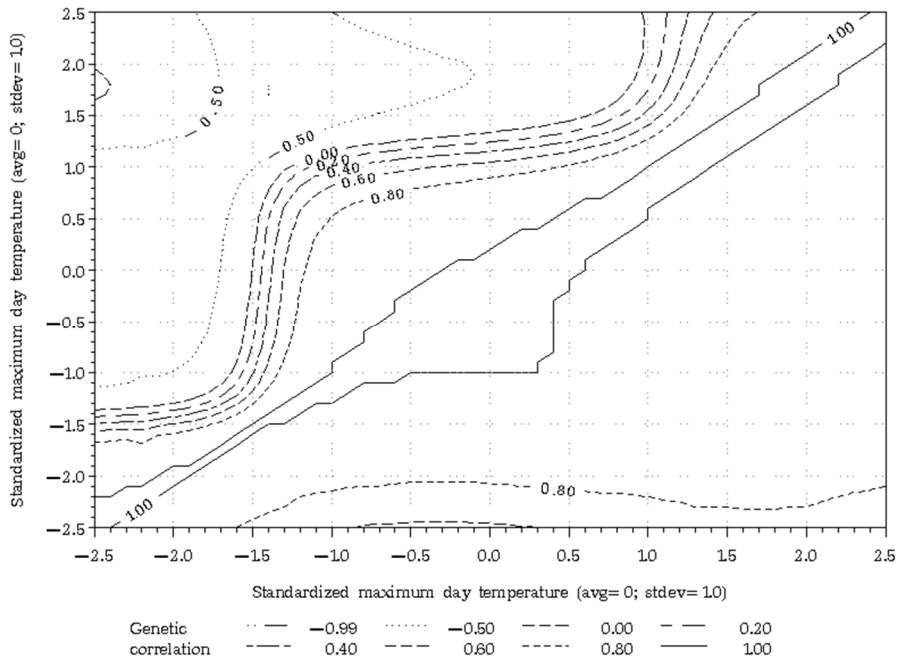
Figure 7.9 Genetic correlations between daily feed intakes during lactation at different temperatures. Above the diagonal temperature correlations exclusively. Below the diagonal the overall genetic correlations at day 21 of lactation.

triangle of Figure 7.9 shows that the overall genetic correlation between different temperature classes was high due to the high influence of additive genetic (co)-variance of day. The upper triangle shows a steep decrease of the genetic correlation between temperature classes as the distance increases. The covariance between temperature classes remained positive within one standard deviation (+/-) of the temperature class (Figure 7.9). For a larger distance the covariance became negative and the correlation between temperature classes decreased to about -0.35.

7.4 Discussion

Phenotypic results

Batch was used to account for differential effects such as management associated with the grouping. In addition, batch was at least partly confounded in this study with temperature, humidity and day length change. To prevent solving problems,

batch was assigned a random effect which has been shown to also benefit smaller contemporary group sizes (ie. Van Vleck, 1987).

In the current study, sows were kept indoors in relatively small units where the ambient room climate was controlled by isolation, indirect air inlet, mechanic ventilation and heating (when necessary). Nevertheless, the external climate had a considerable effect on feed intake of lactating sows. Outside temperature, measured at the nearest weather station, had only a relationship with ambient room temperature when minimum indoor temperature was exceeded because no air cooling was applied and ventilation can, in the long run, not prevent ambient room temperature to rise. The relationship between outside humidity and ambient room humidity will be higher compared to the relationship between outside and inside temperature, because the exhaust fan reacted on temperature and not on humidity. Inlet air was heated at low temperatures and consequently relative humidity dropped within the farrowing shed. At high outside temperatures no heating or cooling of inlet air took place. The combined effects of these interactions might have contributed to the temperature by humidity interaction found in this study.

Ambient room temperature and ambient air quality within a room was partly related since in mechanically ventilated rooms, high ambient room temperatures leads to high ventilation rates. To prevent energy losses, ventilation capacity was lowered at lower temperatures until it reached its minimum ventilation rate, which may have led to lower air quality since air quality is expected to improve with higher ventilation rate. Increased ventilation rate also increases the airflow over the animals and assists with additional cooling. A repetition of our study in a less climate controlled environment would show whether the effect of temperature on feed intake differs compared to conditions where air quality and temperature might not be confounded.

The real effects of high temperature on feed intake during lactation are probably more severe than found in this study. If ambient room temperature reaches heights significantly higher than the desired ambient room temperature, generally management precautions were taken to prevent sows from stop eating. A few precautions one could think of are: prevent animal handling during hottest hours of the day; provide extra water; adjust feeding time so that the first meal was provided earlier on the day and the last meal later in the day. All these measures were implemented at the farm the data originated from and contributed significantly to the lower observed effects.

As mentioned before, pigs regulate their body temperature mainly by increasing or decreasing the blood flow subcutaneously. In case of heat stress, subcutaneous

blood flow will increase and as a consequence blood flow will be decreased in the mammary gland (Black et al., 1993). It is expected that the effect of high temperatures on milk yield will be more severe than the effect on feed intake impacting considerably on piglet development and growth.

Phenotypic and genetic analyses in this study show that high as well as low (outside) temperatures affect feed intake during lactation. Most other studies focus on heat stress or heat tolerance (e.g. Quiniou and Noblet, 1999; Bloemhof et al., unpublished data), probably because pig production is spreading to climates where hot rather than cold thermoregulation is the critical issue.

Random regression

In a dataset, which overlaps to a large extent with the one of the present study, heritability of average (restricted) feed intake over the entire lactation was estimated as 0.14 and the repeatability as 0.23 (Bergsma et al., 2008). In this study, average heritability over the lactation and especially average repeatability, ignoring a genetic temperature response, was higher with estimates of 0.22 and 0.64, respectively applying a random regression on day in lactation and fitting batch as a random effect, which reduced ratios due to the higher phenotypic variance. A similar phenomenon was found by Lewis et al. (2010) who presented a heritability estimate of 0.17 based on random regression analysis of daily feed intake during lactation in comparison to a much higher repeatability of 0.74 due to the larger permanent environment effect of the sow. In beef cattle, the temporary environmental variance was predominantly partitioned into the animal permanent environment effect rather than the residual variance for weight over age using random regression models (Albuquerque and Meyer, 2001). In addition, a fifth versus a seventh order model for additive genetic and animal permanent environment effects increased the permanent environment effect and decreased the additive genetic effect in the beef data. In comparison, a lower order model was applied in our study which may have contributed to higher permanent environment effect of the sow (animal). However, each extra order for the polynomial for feed intake on day in lactation, from the first order to the fourth order, reduced the residual variance significantly, which was also observed for the first until the third order polynomial on temperature at the day of feed intake.

Lewis et al. (2010) performed a similar analysis for *ad libitum* feed intake over 28 day lactation, applying Legendre polynomials, having either day of lactation as the regression trajectory variable, or 24 hour average of the raw air temperature. They studied zero to fifth order polynomials. A second order polynomial (quadratic) was

found sufficient for day of lactation and a first order term (linear) was sufficient for temperature for both fixed and random terms.

Kolmodin et al. (2003) and Van der Waaij (2004) suggested that selection for high productivity in a non-limiting environment resulted in an increased environmental sensitivity, thus suggesting a negative genetic correlation between the intercept and slope of the reaction norm model. Our study did not include the additive intercept for temperature. Therefore, the covariance between the additive intercept and slope of the temperature effect could not be estimated. Once we extended Model 1 in PROC MIXED of SAS with a temperature (and T^2) by sow interaction, computer capacity was not large enough to estimate the effects for the entire dataset. However, for the largest sow cross only (sow cross D in Figure 7.5), the correlation between the level and the slope (linear and quadratic) was not significantly different from zero (results not shown). This correlation indicates that a higher feed intake of sows was not associated with higher sensitivity to temperature (environmental sensitivity).

For simplicity, the order of polynomials was chosen to be the same for all the random effects on day or on temperature dependent feed intake. Pool et al. (2000) concluded that the additive genetic effects require a lower order of Legendre polynomials than the permanent environment effects for milk yield in dairy cattle.

Legendre polynomials generate a weight function with comparatively heavy emphasis on records at the outer parts of the interval for which they are defined compared to other functions (Meyer, 1998). Only a small number of observations for extreme temperature values were available. The extreme variances after day 24 of lactation and at high and low temperatures for the additive and permanent environment effect of temperature response on feed intake might originate from this phenomenon.

The additive variance for feed intake at different days of lactation increased from start of lactation until a maximum at day 20 was reached and decreased afterwards. The curve for animal variance followed the lactation curve. Heritability though, might be highest during the first week of lactation. Various studies report higher heritabilities as the environment became more challenging (i.e. Pollott and Greeff, 2004; Bloemhof et al., unpublished data). Apparently, this also holds for feed intake during lactation. For example, Bunter et al. (2010) found a higher heritability for lactation feed intake in medicated sows compared to un-medicated sows. Medication will predominantly be applied at start of lactation following parturition, when sows are most vulnerable due to the stressors of parturition and the progress of sows from an anabolic state before farrowing to a catabolic state after parturition. At the farm the dataset originates from, sows were fed a high

fiber diet during gestation and a high energy diet during lactation. Digestion of sows had to adapt to these different diets. Changing diets is one of the risk factors for the occurrence of the MMA (Mastitis, Metritis, Agalactia) syndrome. The occurrence of this syndrome is heritable ($h^2=0.13$) as shown by Krieter and Presuhn (2009). Further, transition from colostrum to milk production takes place in the first week of lactation adding to the physiological changes sows experience during the first week of lactation. Heritability estimates varied only minimally ($\sim$0.03 to 0.06) during lactation in the study of Lewis et al. (2010) which used ad libitum feed intake of sows.

Hermesch (2007) studied lactation feed intake over different stages of lactation through average feed intake from day 1 to 5, day 6 to 10, day 11 to 15 and day 16 to 20. The corresponding heritabilities found were 0.02, 0.17, 0.14 and 0.12 respectively. Contrary to the findings applying random regression models, heritability was considerably lower in the first week of lactation with a non-significant estimate of 0.02 ± 0.02. If we repeat this exercise for the dataset in the current study, the heritability for the cumulative amount of feed during the first, second, third and fourth week of lactation was 0.05, 0.09, 0.18 and 0.12 respectively. Different conclusions based on either random regression analysis or weekly cumulative (or average) feed intake seems to originate from different statistical properties between both approaches. For example, random regression analyses use data across the whole trajectory which is ignored in univariate analyses of mean feed intake defined for specific periods of lactation.

Estimation of heritability and temperature sensitivity of feed intake during lactation, applying random regression models is complex but yields favorable results. If the higher heritability of feed intake during the first week (few days) of lactation was the result of the more challenging circumstances during that period, one can hypothesize that this is caused by heritable environmental sensitivity other than heritable temperature sensitivity. This raises the question whether it is possible to select for reduced specific environmental sensitivity.

Alternative approaches

Selection for reduced variation in feed intake

Next to reaction norm models, there is a second approach to reduce environmental sensitivity, the conventional approach to explicitly define a fitness trait (Knap 2005). Such a trait could be variation in day to day feed intake during lactation. If the effect of sow *n* is expelled from Model 1, the residual of every record (day) could be estimated applying Model 1. The new fitness trait could be defined as the standard deviation of the residuals per lactation. Animals who are less

environmental sensitive are expected to show a lower standard deviation. Highly sensitive animals are expected to demonstrate their sensitivity by a large difference in feed intake between days and thus show a high standard deviation. This approach ignores the underlying mechanism of variation of feed intake, but fits the definition of robust animals, which were defined as "pigs that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions" (Knap 2005). Feeding sows restrictively reduced the standard deviation of feed intake per lactation artificially, which may explain the low heritability of the standard deviation of the residuals per lactation found in this study of 0.07 (±0.03) and the low repeatability of 0.14 (±0.02). In addition, the standard deviation in feed intake was genetically the same trait as the average feed intake further reducing the usefulness of this trait as a selection criterion for reduced environmental sensitivity.

Selection against heat stress applying a linear plateau model
Sows are exposed to heat stress when temperature exceeds the upper critical temperature (UCT) of the sow's thermo-neutral zone. The thermo-neutral zone is the zone between the animal's lower and upper critical temperature in which no extra energy is expended to maintain body temperature. It could be hypothesized that reproductive performance of sows is unaffected within the thermo-neutral zone and starts to decrease when temperature exceeds the UCT.

An approach to model environmental sensitivity which corresponds to the theory of Black et al. (1993) was proposed by Ravagnolo and Misztal (2000). They extended a test day model for milk yield in dairy cattle with different rates of production decline with increasing temperatures. Their assumption was that the relative daily production of a cow is unaffected over a range of low and medium temperatures and then starts to decrease after a threshold, the upper critical temperature, assuming that genetic variability in susceptibility to heat stress exists. Bloemhof et al. (2008, unpublished data) demonstrated that such a model is applicable in pigs for reproductive performance as well.

The implicit assumption underlying the model of Ravagnolo and Misztal (2000) is that the genetic correlation in temperature response at different temperatures above the upper critical temperature is high. As the results of the current study demonstrate, this might not always be the case. For that reason it is doubtful whether their model is applicable for lactation feed intake in sows. Taking an additive temperature response into account while estimating breeding values for feed intake during lactation reduces the error variance and thus improves accuracy

of the breeding values. The approach of Ravagnolo and Misztal (2000) benefits from this phenomenon only beyond the upper critical temperature.

Concluding remarks

(i)   Day length changes, humidity and temperature influence lactation feed intake in this order. Differences in temperature might cause differences in feed intake as large as 53 g/d. Differences in humidity can cause differences in feed intake as large as 145 g/d. At start of autumn sows eat 360 g/d less then at start of spring.

(ii) Appropriate higher order polynomial random regression models revealed a considerable permanent environmental effect for the influence of temperature on lactation feed intake. Genetic variance was significant, and size of the variance around a fourth of the permanent environment.

(iii) Breeding for reduced thermal sensitivity of feed intake in lactating sows is possible, even in a controlled environment of a farrowing facility located in a temperate climate zone. The animal that showed the largest drop in feed intake at 28.8 °C ($\overline{x} + 2\sigma$) compared to feed intake at -0.4 °C ($\overline{x} - 2\sigma$) and ate 1.34 kg/d less at 28.8 °C, representing the additive genetic temperature effect (breeding value) plus the permanent environmental temperature effect of that particular animal.

(iv) Statistical models become extremely complex. Random Regression models are a useful tool to quantify the effect of temperature on feed intake during lactation and results can be used to develop less complex models that can be implemented in practical breeding programs. Results may be specific to each environment and therefore environments need to be described clearly.

Acknowledgements

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8

General discussion

8.1 Introduction

The main goal of this thesis was to investigate the need to adapt pig breeding programs that aim at sows that produce more piglets without detrimental effects on the sows and on traits of growing pigs. Traits important for competitiveness of pork in the food market should be maintained and where possible improved. The adaptations of the breeding program should also ensure that the sows maintain their structural soundness. Feed intake is regarded as the driving force behind production of the sow, and lactation is the most energy demanding period in a sow's life. The consequences of the present breeding programs for lactation performance traits, including lactation feed intake, were not fully understood at the start of this study. This thesis focuses mainly on the genetic aspects of feed intake in lactating sows and its relationship with piglet production.

This discussion in this chapter is divided in four sections. The first section (8.2) discusses the phenotypic differences between sows with high and low performance characteristics. By comparing the top 10% with the bottom 10% of observations, linear and non linear relations might become visible to indicate the opportunities and risks of genetic selection.

In the second section (8.3) the consequences of alternative breeding programs are investigated by means of simulation. Besides growing-finishing and reproduction traits, also lactation performance traits were included in the evaluation. In previous chapters of this thesis, genetic correlations between lactation performance traits and reproduction traits (Chapter 3) or growing-finishing traits (Chapter 6) were estimated. In this second section the genetic correlations between growing-finishing traits and reproduction traits are estimated and used in exploring the consequences of alternative breeding programs.

In the third section (8.4) the ethical considerations regarding pig breeding companies are discussed. Attention is paid to increasing concern about physiological limits of genetic selection and improved husbandry. Current breeding programs improve market pig performance and reproduction efficiency. As a consequence, feed intake capacity in growing pigs tends to decrease and feed efficiency tends to increase. Increased production and feed efficiency will reduce the ecological foot print of pig production. On the other hand there might be a limit to reduction in feed intake since it might have undesired effects on animals functioning. This dilemma is addressed in section 8.4. Finally, in the fourth section (8.5) the conclusions from the three sections will be combined into a general conclusion.

8.2 Phenotypic consequences of selection

Data have been obtained from the last five years of the experimental farm of IPG (for detailed description see textbox [Box 8.1] below). The dataset was divided into five classes, as a technique to demonstrate the phenotypic consequences of unilateral genetic selection. The data were placed in ascending order according to the characteristic of interest (the selection criterion). The 10% lowest observations formed the first class, the 20% adjacent observations the second class, the next 40% the third, the following 20% formed the fourth class and finally, the last (highest) 10% of the observations for a trait formed the fifth and last class.

The difference between the averages of the top 10% and bottom 10% observations is ≈3.3 phenotypic standard deviations, assuming observations are normally distributed. This difference represents 6.6 generations of selection, in case of unilateral genetic selection on a trait with a heritability of 0.25, achieving a genetic progress of 0.5 genetic standard deviation per generation. Moving from the average towards the top 10% or bottom 10% equals 5 years of genetic selection, in case of a generation interval of 1.5 years.

In this section, six different traits were discussed. The first two, weight loss of sows during lactation and leanness of sows, were considered a consequence of current selection strategies. Next to these, four other traits which have been considered throughout this thesis as alternative selection criteria: sow feed intake during lactation, milk yield, piglet's birth weight and lactation efficiency, will be discussed. The latter four are also included in the simulation study of section 8.3.

The tables in the text (8.2, 8.3, 8.4, 8.7, 8.8 and 8.9) contain only a selection of traits. They are accompanied by a comprehensive version in the appendix (A8.2 to A8.7).

Motivation of the present research

In the general introduction of this thesis, it was already pointed out that current breeding programs in dam lines may increase the risks of a too large negative energy balance in sows during lactation, with severe body tissue mobilization as a consequence. Excessive body tissue mobilization may affect fertility and productivity of the next cycle. Especially protein mobilization is considered a risk. So far only literature was reviewed to substantiate this claim.

Table 8.2 shows the relationship between weight loss during lactation and other traits. The 10% lactations with the lowest weight loss, gained 5.3 kg during lactation. The 10% lactations with the highest weight loss lost a little over 33 kg weight, a difference of almost 40 kg. From the observations on weight and backfat

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Box 8.1 Materials and methods phenotypic consequences of selection

A large part of the research presented in this thesis is based on data of the research farm of the Institute for Pig Genetics (IPG). This chapter is no exception. In this section, the consequences of selection for a number of fertility and lactation performance traits are analysed. Detailed definitions of the traits, presented in this section, are given in Chapter 2. The majority of the data originates from September 2003 until February 2009. During lactation, sows were fed restricted at that time. More details on the feeding strategy are given in Chapter 7.

The dataset was divided into five classes. The data were placed in ascending order according to the characteristic of interest (the selection criterion). The 10% lowest observations formed the first class, the 20% adjacent observations the second class, the next 40% the third, the following 20% formed the fourth class and finally, the last (highest) 10% of the observations for a trait formed the fifth and last class. Before sorting, the observations were (pre-) corrected for the genetic line of the sow, the parity of the sow and the contemporary group (HYS) of the litter (and lactation length if appropriate) to maximize the chance that these effects are equally distributed over all five classes.

Least Squares Means and significance levels for the five classes for all dependent traits were obtained using PROC MIXED in SAS/STAT software (SAS, 1999). Three different models were used.

$$Y = \mu + CLASS + PARITY + \underline{HYS} + \underline{SOW} + e \tag{1}$$
$$Y = \mu + CLASS + PARITY + b_1 \cdot LLE + \underline{HYS} + \underline{SOW} + e \tag{2}$$
$$Y = \mu + CLASS + b_1 \cdot LLE + \underline{HYS} + e \tag{3}$$

where: y=the observed phenotype; μ = population mean; CLASS=the class-effect, defined as the 10-20-40-20-10 % of the observations; PARITY = the parity of the sow, parity six and higher were combined; HYS = Herd-Year-Season = three weeks batch of farrowing (random); LLE = Length of lactation, d; SOW=the (random) effect of the sow. Because of repeated observations (different litters), a particular sow or sow family can have a major impact on one of the classes. Therefore, the random effect of the sow was included. The random effect of the sow also takes into account the effect of the genetic line of the sow; e = residual.

Note that observations were two times subjected to a statistical analysis. Firstly to obtain residuals used for classification. Secondly the original observations were used again to obtain Least Squares Means. In the latter situation Model (1) to (3) were used. Traits which were recorded before weaning were analysed applying Model 1. For traits recorded at or after weaning, lactation length was added to the model (Model 2). For stayability (1st litter survival of sows), the random effect of the sow was removed from the statistical model because (by definition) only 1 observation per sow was available (Model 3). In case Model 2 was applied, Least Squares Means were estimated assuming a lactation length of 25 days. Only lactations that were completed with weaning of piglets at a minimum age of 14 days were selected. 1.5 % of the litters did not fulfil this criterion. Differences between sows that completed their lactation and did not are depicted in Table 8.1. Higher parity sows had a higher chance not to complete their lactation. These sows gave birth to an average number of piglets but the piglets had a lower birth weight, were born at an earlier gestation stage and especially their percentage stillborn piglets was higher. Unequal distribution of unsuccessful lactations over the various classes might affect the results. Since it only concerns a small number of observations, the impact of removing incomplete lactations from the dataset is considered small and is ignored further on.

Box 8.1 Materials and methods phenotypic consequences of selection (continued)

Table 8.1. Difference between completed and uncompleted lactations (uncorrected means).

	Lactation completed	Lactation not completed
No of farrowings	2049	31
Parity (mean)	3.4	4.1
Empty weight sow at farrowing, kg	224	235
% fat at farrowing	20.7	20.6
Gestation length, d	115.7	114.6
Total number born	13.4	13.5
Stillborn, %	6.1	23.2
Litter weight before cross fostering, kg	18.4	16.7

thickness, fat mass and protein mass were estimated (Chapter 2). Weight, fat mass and protein mass are therefore correlated. In fact the phenotypic correlation between weight loss and protein loss over the lactation is +0.96 (Table 3.4). Weight loss is presented in Table 8.2, but, because of the high phenotypic correlation, conclusions hold for protein losses as well. Consequences of measurement errors of the estimated traits have been discussed in Chapter 2.

Sows that lost most weight during lactation were heavier at start of lactation. Their total number of piglets born was lower. Since litter mass was unaffected, average birth weight of piglets was higher in sows that lost most weight. Litter uniformity was unaffected. After cross fostering, the number of piglets to be nursed was more evenly spread over the five classes but still sows that lost most weight had the least number of piglets to nurse. Those piglets were significantly heavier at birth though. Sows that lost most weight showed a decreased feed intake but an increased milk yield. The 10% lactations with the highest weight losses showed a 24% increased milk yield compared to the 10% lactations where sows gained weight. Higher milk yield was associated with decreased mortality and thus increased number of piglets weaned. Lactation efficiency was unaffected. Interval weaning to estrus, farrowing rate and total number of piglets born in the next parity were not affected either. High weight loss did not lead to a higher culling rate (counterpart of survival current cycle).

Primiparous sows are the most vulnerable group of sows. Mostly, these sows have to nurse an equal number of piglets as their number of functional teats, which is higher than the number of piglets a multiparous sow has to nurse. Feed intake capacity of primiparous sows is lower than of multiparous sows. Primiparous sows

Table 8.2 Least Squares Means of sow performances ordered and grouped according to their weight loss during lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Weight loss is pre-corrected for genetic line, parity of the sow, Herd Year Season and lactation length.

Trait	Classification: Weight loss [1]				
	10% *lowest*	*20%* *low*	*40%* *average*	*20%* *high*	*10%* *highest*
Number of lactations	198	397	793	397	199
Weight loss during lactation, kg/25 d	-5.3	6.7	16.1	25.0	33.1
Empty weight sow at farrowing, kg	221[a]	225[b]	229[c]	234[d]	237[e]
Backfat thickness at farrowing, mm	17.4[a]	17.9[b]	18.4[c]	18.9[d]	19.3[d]
Fat to protein ratio at farrowing	1.31[a]	1.33[a]	1.35[b]	1.36[bc]	1.38[c]
Total number born	14.2[a]	13.9[a]	13.4[b]	13.2[bc]	13.0[c]
Number of piglets to be nursed	12.4[a]	12.2[ab]	12.0[bc]	11.9[c]	12.0[bc]
Avg. birth weight after cross fostering, kg	1.31[a]	1.35[a]	1.44[b]	1.51[c]	1.58[d]
Feed intake during lactation, kg	133[a]	132[a]	130[b]	126[c]	119[d]
Adjusted weaning weight sow, kg	226[a]	219[b]	214[c]	210[d]	204[e]
Backfat thickness at weaning, mm	15.3[a]	15.1[ab]	14.9[b]	14.8[bc]	14.6[c]
Fat to protein ratio at weaning	1.15[a]	1.15[a]	1.15[a]	1.16[a]	1.16[a]
Pre-weaning mortality, %	19.8[a]	14.2[b]	10.5[c]	8.2[d]	7.1[d]
Number of piglets weaned	9.7[a]	10.3[b]	10.6[c]	10.9[d]	11.1[e]
Milk yield, MJ ME/d	47.5[a]	51.7[b]	54.9[c]	56.3[d]	57.8[e]
Lactation efficiency, %	75[a]	75[a]	75[a]	74[a]	75[a]
Survival current cycle, %	76[a]	81[b]	85[c]	83[c]	83[c]
Prolonged interval weaning-estrus, %	8.5[a]	8.4[a]	10.8[a]	8.9[a]	7.6[a]

[1] Classes within rows with no common letter as suffix, differ significantly (p<0.05).

have not yet reached their full mature weight, which means that they have less body reserves and are still supposed to grow. If an impact of weight losses is to be expected, this is certainly the case in the primiparous sows. But even in the primiparous sows, no negative effect of weight losses on fertility and productivity of the next litter could be proven at the IPG-farm (results not shown). The 10 % primiparous sows that lost least weight, gained on average 2.1 kg (n=40). Those which lost most weight lost 34.2 kg (n=41). The difference between both most extreme groups of primiparous sows (36.3 kg) was almost as large as across parities (38.4 kg).

In Chapter 3 it was already concluded that "A breeding objective for dam lines with emphasis on total number born, pre-weaning mortality and % prolonged interval weaning – estrus will not dramatically change body weight and body composition at start of lactation, and mobilization of body tissue and feed intake during

lactation. Present levels of performance, expressed as number of piglets weaned per sow per year, are not a risk for stayability of sows." Whereas rather large weight losses did occur, even in primiparous sows, apparently management strategies exist to cope with these weight losses while maintaining acceptable levels of performance. In the Appendix (Table A8.1), production numbers of the IPG-farm are compared against the performance of the average group of farmers in the Netherlands. Based on number of piglets weaned per sow per year, the IPG-farm performed above average whereas the percentage primiparous sows was also above average.

In data obtained from the IPG-farm, no negative effect of high weight losses on fertility traits of the next parity could be proven, which was unexpected. The 10% sows that lost most weight, lost almost 14% of their body weight during lactation. They had 14.6 mm of backfat at 204 kg of weight, which is considered a good condition at weaning. Clowes et al. (2003a) demonstrated that at weaning ovarian function was suppressed in those sows that had mobilized the most body protein. Their data suggest no decline in lactational performance or ovarian function when a sow loses approximately 9 to 12% of her parturition protein mass. They also concluded that ovarian function at weaning was higher in high body-mass sows, suggesting that a larger lean mass may delay the onset of a decrease in performance in sows that loose protein in lactation (Clowes et al., 2003b). The 10% sows that lost most weight in our comparison, lost 13% body protein during lactation, which is marginally different from the 9-12% reported by Clowes et al. (2003a). These sows were also the heaviest sows (in absolute weight and in protein mass) at the start of lactation. From that perspective it was perhaps less unexpected that no negative effect of weight loss on the sows was found at the IPG farm.

Reproductive failure after weaning has two possible biological backgrounds according to Kemp and Soede (2004) in a literature review: (1) Impaired LH levels during lactation; and (2) impaired follicle development during (and after) lactation. Both phenomena originate from lysine (as most limiting amino acid) and/or energy deficiencies during lactation.

Directly after weaning, in good reproductive sows, LH production is characterized by a high frequency/low amplitude pulse frequency which induces recruitment of the then existing population of large follicles. Sows in which LH pulsatility was not restored during lactation showed impaired LH levels and pulse frequencies directly after weaning (called suppressed ovarian function by Clowes in the previous paragraph) and a prolonged weaning to estrus interval. It seems therefore that the ability of sows to increase levels of LH during lactation is important for a short

weaning to estrus interval. Mean LH at day 21 of lactation is reduced by restrictions of either lysine or energy intake.

The causes for a reduced litter size in the subsequent parity or a lower farrowing rate can be found in low ovulation rates or a high embryonic mortality. Kemp and Soede (2004) suggest that low feeding levels during lactation impair follicle development during and after lactation resulting in a lower number of follicles recruitable for ovulation (which results in a lower ovulation rate) and an impaired quality of eggs and follicular fluid (which may explain increased embryonic mortality). A lower ovulation rate and an increased embryonic mortality may both result in lower litter sizes at parturition. When ovulation rate is low or embryonic mortality is high, the number of embryos may be below the minimum of two per uterine horn. This minimum is required around day 10-15 of pregnancy for maternal recognition of pregnancy. In that case sows will not remain pregnant and return to estrus after 21 days. Restricted feeding seems to restrict follicle growth during lactation with consequently affects follicle development after lactation. It might very well be that genetic selection for reduced interval weaning to estrus, increased litter size and/or increased stayability, reduces vulnerability of LH levels and follicle development for a high negative energy balance in modern sows.

Sows that belonged to the lowest weight loss group during a 25 day lactation period, gained on average 5.3 kg of weight of which 1.6 kg of protein (see Table 8.2). They lost 3.3 kg of fat though. Sows in the adjacent category (20% low weight losses) already lost protein. After farrowing sows start to produce colostrum. The colostral phase is characterized by a large export of protein into the milk. Assuming that the ratio of colostrum consumption to piglet weight gain is 2.4 and the mean concentration of protein in colostrum is 100 mg/g, total export of protein through colostrum during the first 24 h ranges from 260–600 g (Le Dividich et al., 2005), which is equivalent to approximately 1.8 – 3.0 kg muscle. Due to the low feed intake of the sow soon after parturition, this export probably results in a high rate of the sow body protein catabolism even though most colostral immunoglobulins originate from sow blood plasma (Le Dividich et al., 2005). Some studies found evidence that the physiological state of pregnancy enhanced protein deposition in the maternal body. Enhanced protein deposition during gestation might facilitate the large export of protein during the colostral phase. Other studies denied this phenomenon and found that the increase in protein deposition during pregnancy was entirely associated with deposition in the reproductive tissue (Close et al., 1985).

In Figure 8.1 the distribution of fat and protein over weight loss is depicted in case of a negative energy balance during lactation (Energy balance = Energy through
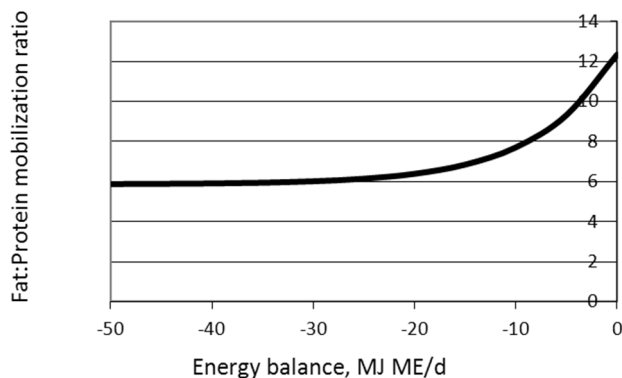
Figure 8.1 Ratio of fat and protein mobilization during lactation in case of a negative energy balance.

feed intake – energy needed for maintenance – energy needed for milk production).

In case of a very small negative energy balance, sows mobilized mainly fat. But even then, sows already mobilized some protein since the fat to protein ratio never got higher then 12. Towards a high negative energy balance the proportion protein losses increased. Nevertheless, the ratio did not drop below 6. The fat to protein ratio in body tissue mobilization also depended on fatness of a sow at start of lactation. The 10% sows that lost most weight during lactation had a higher fat to protein ratio in their body at start of lactation than sows that lost less weight. At weaning though, all five categories showed a similar fat to protein ratio, despite different weights. It might well be that the minimum or optimum fat to protein ratio is the driving force behind body tissue mobilization. Whittemore and Morgan (1990) concluded that lactating sows appeared unwilling to mobilize fat stores when (P2) backfat falls below 10 mm and when the lipid to protein ratio in the whole body falls below 1 to 1. This suggests that the remaining fat is structural fat and that lean genotypes of sows may be less likely to mobilize from body stores for milk production than fatter genotypes.

The optimum fatness of a sow at start of lactation
Body fat plays an important role in lactating sows. Fat provides easy accessible energy and the general feeling of piglet producers is that sows need a certain amount of body fat to ensure a trouble-free lactation. This feeling is not well substantiated though. Selection for lean meat in grower-finishers will reduce the body fat reserves of sows (Chapter 6). If sows need a minimum amount of body fat

at the start of lactation, selection in dam lines for lean meat as a grower-finisher should be accommodated.

Table 8.3 shows that sow with a high fat mass at start of lactation appeared to have both a lower litter size and litter mass at birth. This phenomenon was found in other studies as well (e.g. Bunter et al., 2010). Fat sows were also the heavier sows. The high fat mass and weight at start of lactation in sows with a reduced litter size was considered to be a cause of a reduced number of fetuses, because more energy was available for maternal gain.

In Table 8.2 the consequences of weight losses are depicted. It was suggested that animals apparently strive for an optimum fat to protein ratio at weaning. If that is true then data in Table 8.3 show that the optimum level of the fat to protein ratio at weaning depends on the fatness (leanness) of an animal at farrowing. The fat to protein ratio at weaning is increasing with increased fat to protein ratio at farrowing. The suggestion of Whittemore and Morgan (1990) that lean genotypes of sows may mobilize less tissue from body stores for milk production than fatter genotypes is also clear from Table 8.3. One could also argue that the necessity for lean sows to mobilize body tissue was absent. Lean sows compensated for their smaller fat stores by eating more and be more (energy) efficient. Output was equal for all five classes.

Stillbirth

Some authors suggested that sows which are very fat at parturition have a high risk to suffer from dystocia and associated high stillbirth rate, agalactia, mastitis and metritis (Göransson, 1989; Weldon et al., 1994a), The correlation between the incidence of agalactia and the number of still-born piglets per litter can perhaps be explained by a prolonged duration of time for labor of the sows. High backfat levels in our dataset were not detrimental for number of stillborn piglets. In fact, the 10 % fattest sows showed the lowest percentage stillborn piglets.

Leenhouwers et al. (2002) provided a possible explanation for the reduced percentage stillborn piglets. In their study, a higher % carcass fat and a higher average serum cortisol concentration was found in piglets with a high genetic merit for survival (prenatal and from birth to weaning) after being delivered by Caesarean section at, on average, day 111 of gestation. Differences in cortisol are known to affect lung maturation and glycogen synthesis, both important for early survival. High percentages of carcass fat in piglets and associated cortisol levels probably reduced the percentage stillborn piglets.

The relation between fatness of the sow and cortisol levels of the piglets holds under the assumption that fatter sows also produce piglets with a higher % carcass

Table 8.3 Sow performances (Least Squares Means) ordered and grouped according to their fatness at start of lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Percentage fat is pre-corrected for genetic line, parity of the sow and Herd Year Season of the litter.

Trait	Classification: % Fat [1]				
	10% *leanest*	*20%* *lean*	*40%* *average*	*20%* *fat*	*10%* *fattest*
% fat at farrowing	16.3	18.3	20.6	22.9	25.5
Empty weight sow at farrowing, kg	218[a]	226[b]	229[c]	234[d]	236[e]
Back fat thickness at farrowing, mm	13.1[a]	15.7[b]	18.2[c]	21.1[d]	24.1[e]
Fat to protein ratio at farrowing	1.01[a]	1.17[b]	1.33[c]	1.52[d]	1.73[e]
Total number born	13.8[ab]	13.9[a]	13.4[b]	13.4[b]	13.2[b]
Stillborn, %	6.8[a]	7.0[a]	6.0[ab]	6.7[a]	4.9[b]
Litter weight before cross fostering, kg	19.0[ab]	19.0[a]	18.5[bc]	18.2[c]	18.3[bc]
Number of piglets to be nursed	12.2[a]	12.2[a]	12.0[a]	12.1[a]	12.0[a]
Litter weight after cross fostering, kg	17.5[a]	17.2[a]	17.1[a]	17.2[a]	17.1[a]
Feed intake during lactation, kg	132[a]	131[a]	129[b]	127[bc]	125[c]
Adjusted weaning weight sow, kg	208[a]	212[b]	215[c]	217[d]	220[e]
Back fat thickness at weaning, mm	11.8[a]	13.3[b]	14.9[c]	16.6[d]	18.1[e]
Fat to protein ratio at weaning	0.95[a]	1.05[b]	1.15[c]	1.27[d]	1.37[e]
Weight loss during lactation, kg	11.7[a]	14.5[b]	14.7[b]	16.4[c]	15.1[bc]
Fat loss during lactation, kg	4.4[a]	6.3[b]	7.9[c]	10.0[d]	12.3[e]
Protein loss during lactation, kg	1.5[a]	1.7[a]	1.5[a]	1.5[a]	0.9[b]
Pre-weaning mortality, %	12.4[a]	12.1[a]	11.3[a]	10.6[a]	11.7[a]
Milk yield, MJ ME/d	53.8[ab]	54.0[ab]	53.9[ab]	54.7[a]	52.8[b]
Lactation efficiency, %	78[a]	76[a]	76[a]	74[b]	70[c]
Survival current cycle, %	80[a]	83[a]	83[a]	82[a]	83[a]
Prolonged interval weaning-estrus, %	5.2[a]	8.5[ab]	10.5[b]	9.8[ab]	9.7[ab]

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

fat. Development of an animal is a process that starts at fertilization and ends at maturity. Different growth phases are auto-correlated because of the underlying development processes. This is especially valid for fat content since the heritability is high and the genetic correlations between fatness during different phases in life is high as well, whereas composition of the fetal pig has been shown to be less affected by manipulating sow diet (Herpin et al., 1993). Thus, as sows become fatter, their piglets will become fatter as well. Cortisol levels remain associated with fatness, also later in life. Foury et al. (2007) found a significant positive relationship between basal cortisol levels and fatness at slaughter weight. If farrowing survival of piglets depends on their % carcass fat, one might expect that

percentage stillborn piglets increase with increasing leanness of sows. There are studies that support this theory. Maes et al. (2004) for instance, investigated three different sow herds. Sows with low amounts of back fat at the end of gestation experienced a significantly higher percentage of stillborn piglets in one of the three investigated herds and to a lesser extent in another herd (p=0.069).

Our study, however, did not show a higher risk for still birth as sows became leaner. From the 10 % fattest sows there was a fall back in farrowing survival of piglets. Moving towards leaner sows did not significantly increase percentage stillborn piglets.

Litter weight

Piglet's birth weight is of growing concern in the pig husbandry since low birth weight negatively affects growing-finishing performance (Herring et al., 2010; Beaulieu et al., 2010).

It is apparent that the swine industry has continued to increase litter size (see general introduction) and that increased litter size results in lower, individual piglet birth weights (Roehe, 1999; Knol, 2001).

Fatness of sows and litter weight may be associated. If we compare the two leanest categories of Table 8.3 to the two fattest categories, it shows that leaner sows at farrowing had a higher litter weight. Farrowings in the two leanest categories of Table 8.3, however, showed also a slightly higher litter size. As a result the average birth weight (before and after cross fostering) was equal for all five categories. Pre-weaning mortality was not significantly affected by fatness of the sow.

Selection experiments for lean growth in pigs (Vangen, 1972; Kerr & Cameron, 1995) showed that leaner lines had a higher litter weight, primarily due to heavier piglets at birth. Despite an increase in birth weight, mortality from birth to weaning (Kerr and Cameron, 1995) or prenatal mortality (Vangen, 1972) was higher in piglets from these leaner sows. The effect of decreased cortisol levels in leaner piglets may have been associated with this again. Increased pre-weaning mortality may also be attributed to higher restlessness observed in leaner sows (Vangen, 1980; McKay, 1993)

Nor from Table 8.3, neither from our genetic correlations estimates, we could confirm that selection for leaner grower-finishers would increase pre-weaning mortality. Selection for leaner grower-finishers will create leaner sows at start of lactation (r_g=0.53; Table 6.7). Lower fat mass at start of lactation was associated with higher litter weight (r_g=-0.36; Table 3.4). But the direct estimate of the genetic correlation between fat mass at start of lactation and pre-weaning mortality was not significantly different from zero (r_g=-0.13; Table 3.4).

Feed intake

High fat mass at the start of the lactation was associated with low feed intake during lactation (e.g. Mullan and Williams, 1989; Dourmad, 1991; Weldon et al., 1994a). In our example, the difference in feed intake between the 10 % leanest and 10 % fattest sows (at parturition) was 7 kg over a 25 day lactation period (Table 8.3). Reduced feed intake was accompanied by extra body tissue mobilization or extra weight loss (r_p=-0.40 and -0.27 with ad libitum and restricted feed intake respectively; $p<0.05$) (Table 3.4). The direct relation between fat mass at start of the lactation and weight loss was not very pronounced, nor the relation between fat mass and protein mobilization. In Chapter 3 (Table 3.4) we found phenotypic correlations of +0.16 and +0.06 respectively ($p<0.05$). The phenotypic correlation between fat mass and fat mobilization was much higher (r_p=+0.36). Table 8.3 also nicely demonstrated this. Adjacent increasing classes of fatness at the start of lactation showed significant increases in fat mobilization. Protein mobilization seemed independent of fat mass. Fat loss during lactation of the 10% fattest sows was not negatively associated with fertility or prolificacy of the next cycle, since no effect could be found on % prolonged interval weaning – estrus; farrowing rate; total number born and culling rate. The 10% fattest sows lost 12.3 kg of fat, which represented 81% of the total weight loss.

Susceptibility for short live duration

There is a hesitation in selecting for grower-finishing traits in dam lines, especially for lean meat percentage, by users of breeding stock. They fear increased susceptibility of sows. Increased susceptibility will be expressed by decreased stayability. Increased susceptibility was confirmed by various authors who reported an unfavorable relationship between backfat thickness as a finisher and stayability (Tholen and Graser, 1996; López-Serrano et al., 2000). Contrary to our findings, López-Serrano et al. expected that limited possibilities for body fat mobilizations during lactation turn the scale: difficulties in sows becoming pregnant due to a negative energy balance is a possible explanation for the unfavorable relationship between backfat thickness and stayability since reproduction problems are important reasons for culling.

The unfavorable correlation between backfat thickness and stayability could also be explained through a leg weakness syndrome as a consequence of lower backfat thickness (Bereskin, 1979; Webb et al., 1983; Lundeheim, 1987; Von Brevern, 1996). It is in agreement with the unfavorable genetic correlations between backfat thickness and the exterior traits of gait and swinging of the back (r_g = 0.26 and r_g =

-0.11, respectively). Both traits are associated with longevity according to Van Steenbergen (1990).

The frequency of decubitus ulcers (or pressure ulcers) is expected to increase as sows become leaner. Decubitus ulcers are lesions caused by unrelieved pressure, especially over bony areas such as shoulder, hip region and legs. Although treatable if found early, decubitus ulcers are often fatal.

Results of Table 8.3 provided no evidence to support the idea of susceptibility as sows become leaner, since no effects of leanness on survival rate, on percentage prolonged interval after weaning and on farrowing rate of the first insemination after weaning were found.

Phenotypic and genetic correlation estimates in this area, are difficult to interpret. The genetic correlation between fat mass at start of lactation and stayability after the first litter was positive (r_g=+0.39; Table 3.4). This would support the idea of sows becoming more susceptible to early culling as they become leaner. The most pronounced genetic correlation related to stayability is the one with feed intake during lactation (r_g=-0.60 and -0.92 with ad libitum and restricted feed intake respectively; Table 3.4). The positive genetic correlation of stayability with fat mass and the negative correlation with feed intake during lactation can both be true when fat mobilization during lactation is beneficial for stayability. Fat losses per se did not show a significant genetic correlation with stayability; neither did fat mass at start of lactation with fat losses during lactation. One could argue that fat losses during lactation are heritable to a small extend only (h^2=0.05 ± 0.04; Table 3.1) and genetic correlations with other traits were therefore difficult to estimate.

Efficiency of fat deposition over gestation and lactation

The efficiency of utilization of ME for deposition in maternal tissues in pregnant sows is 75 to 80% (Noblet et al., 1990). The efficiency of utilization of body energy reserves for lactation is considered to be 85%. The combined efficiency of tissue gain during pregnancy and its mobilization during lactation therefore is about 69%. This suggests that the storage of body fat during pregnancy and the subsequent utilization during lactation results in an overall efficiency that is almost similar to the efficiency of direct utilization of ME for milk during lactation (72% according to Noblet et al. shown in Figure 2.1). Similar conclusions were reached by Moe et al. (1971) for dairy cows.

From an energy metabolism point of view, a two step conversion from feed into milk (feed ->body reserves->milk) is unlikely to be as efficient as direct conversion of energy from feed to milk. If the overall efficiency is all the same after all, animals that stored more energy in body reserves during gestation might have been more

efficient for example because they became increasingly inactive and thus spent less energy in activity.

Fat sows don't milk

Table 8.3 shows an interesting phenomenon, which best can be described as: "Fat sows don't milk". From an energy point of view, high feed intake of leaner sows does not fully compensate for the low fat mobilization. There was a tendency of reduced availability of energy from the body for milk production (input) as sows became leaner, as can be seen in Table 8.3. The output on the other hand was constant, except for the fattest sows which showed a significantly reduced litter weight gain or milk yield. Other production traits like pre-weaning mortality or weaned piglets per litter were independent of leanness. Especially the fattest group of sows was energetically inefficient. Head and Williams (1995) reported a significantly reduced litter growth with fat sows. Revell et al. (1998) reported that milk yield was about 15% higher in lean than fat sows, which was also reflected in litter growth. Head and Williams (1991) stated that fat sows, in comparison with lean sows, had a lower capacity to secrete energy in milk because they had fewer milk secretory cells. A lower milk production may diminish the drive to eat and therefore reduce voluntary feed intake of sows. In most other studies, however (e.g. Jones et al., 2006; Weldon et al., 1994a, b; Dourmad, 1991), litter growth was not affected by a high gestation feeding level and high fatness level at farrowing. Contrary to our results, their studies were based on primiparous sows. This may have affected the results.

The 10 % fattest sows showed a significantly lower protein mobilization combined with a lower protein mass at start of lactation (Table A8.3). Feed intake of these sows was reduced as well. Therefore, less protein was available to supply substrates for milk production, compared to lean sows. This also might have caused the reduced milk production. The reduced milk production on the other hand can be the basis for the low protein mobilization.

Table 8.3 suggests that the relation between fatness of the sow at the start of lactation and milk yield during lactation was non linear. That is probably why the genetic correlation between fat mass at start of lactation and litter weight gain was non significant (Table 3.4). However, the genetic correlation between back fat thickness as a grower-finisher and litter weight gain was significant (r_g= -0.27, $p < 0.05$; Table 6.7).

Summary

Summarizing the section on the optimum fatness of a sow, we can conclude that fatness at the start of lactation appears not to affect fertility or prolificacy of the next cycle. Lean sows compensate their inability to mobilize fat stores by a high feed intake and high feed efficiency. Better management skills of farmers are needed to ensure feed intake during lactation if we move towards lean sows. The risk on reduced stayability of lean sows, for example as a consequence of leg weakness and an increased mortality amongst piglets of leaner sows despite increased litter weights, can not be completely ruled out. From an energy efficiency point of view there is hardly any difference between lipid deposition during gestation and mobilization during the successive lactation, or direct energy utilization for milk production out of feed. Extreme fatness however, is detrimental for milk production.

High feed intake sows are energetically inefficient

In Chapter 6 we demonstrated that the genetic correlation between feed intake as a grower finisher and feed intake as a lactating sow was low (r_g=+0.23). Meaning that selection for leaner growing-finishing pigs with higher feed efficiency (and thus reduced feed intake) did not rule out selection for increased feed intake during lactation as proposed by Eissen (2000) to prevent reproductive problems in sows. In Table 8.4, sows are grouped according to their feed intake during lactation.

High feed intake sows tended to be lighter and leaner at the start of lactation which might have been expected from discussing the differences depending on fatness of the sow (Table 8.3). All other characteristics at start of lactation were remarkably similar for all five feed intake classes.

In general, high feed intake prevented body mobilization despite an increased milk yield. For other characteristics than mobilization and milk output, differences between the five feed intake classes were small. Nevertheless one gets the impression that high feed intake sows are easy to manage sows. Number of piglets weaned was a little higher; % prolonged interval benefited although not significant and survival to the next cycle was improved compared to the sows with lowest feed intake during lactation.

The most striking differences between the five feed intake-classes however were found in lactation efficiency which decreased clearly as feed intake increases. This confirms the moderately negative genetic and phenotypic correlation between feed intake (ad libitum and restricted) and lactation efficiency as found in Chapter 3.

Table 8.4 Sow performances (Least Squares Means) ordered and grouped according to their feed intake during lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Feed intake is pre-corrected for genetic line, parity of the sow and lactation length.

Trait	Classification: Feed intake [1]				
	10% *lowest*	*20%* *low*	*40%* *average*	*20%* *high*	*10%* *highest*
Feed intake, kg/25 days	108	119	135	148	156
Empty weight sow at farrowing, kg	233[a]	232[a]	229[b]	227[b]	227[b]
Backfat thickness at farrowing, mm	19.0[a]	18.5[a]	18.1[b]	17.7[c]	17.8[bc]
Fat to protein ratio at farrowing	1.36[a]	1.34[ab]	1.32[bc]	1.31[c]	1.32[bc]
Total number born	13.4[ab]	13.2[ab]	13.0[a]	13.5[b]	13.6[b]
Litter weight before cross fostering, kg	18.6[ab]	18.4[ab]	18.4[a]	18.9[b]	18.8[ab]
Number of piglets to be nursed	12.0[ab]	11.7[a]	11.8[a]	11.9[ab]	12.1[b]
Litter weight after cross fostering, kg	17.1[a]	17.0[a]	17.1[a]	17.3[a]	17.4[a]
Adjusted weaning weight sow, kg	212[a]	216[b]	216[b]	217[b]	218[b]
Backfat thickness at weaning, mm	15.1[ab]	15.1[a]	14.9[ab]	14.8[b]	14.8[ab]
Fat to protein ratio at weaning	1.16[a]	1.16[a]	1.14[a]	1.14[a]	1.14[a]
Weight loss during lactation, kg	21.4[a]	15.5[b]	12.8[c]	10.5[d]	10.2[d]
Fat loss during lactation, kg	9.7[a]	8.1[b]	7.4[c]	6.5[d]	7.0[cd]
Protein loss during lactation, kg	2.4[a]	1.6[b]	1.2[c]	0.9[d]	0.8[d]
Pre-weaning mortality, %	13.3[a]	11.9[a]	11.6[a]	11.8[a]	11.9[a]
Number of piglets weaned	10.2[a]	10.2[a]	10.3[ab]	10.4[b]	10.5[b]
Milk yield, MJ ME/d	49.5[a]	51.7[b]	53.9[c]	54.8[d]	56.5[e]
Lactation efficiency, %	84[a]	79[b]	74[c]	71[d]	68[e]
Survival current cycle, %	77[a]	85[b]	85[b]	85[b]	84[b]
Prolonged interval weaning-estrus, %	8.9[abc]	11.6[a]	9.8[ab]	6.6[bc]	4.2[c]

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

If there is an optimum fat to protein ratio at weaning as has been suggested when discussing weight loss during lactation, this optimum is not affected by the feed intake of the sow during lactation. The fat to protein ratio at weaning was similar for all five feed intake classes. Differences in fat to protein ratio were, however, small at farrowing.

Stayability

Table 8.4 shows that extremely low (restricted) feed intakes were detrimental for survival to the next parity. Sows, of which lactation belonged to the 10% with lowest feed intake, had a significant higher chance to be culled, compared to the four other feed intake classes. In Chapter 3 we found a non significant phenotypic

correlation between restricted feed intake and first litter survival (-0.09) and a small but significant (+0.15) positive phenotypic correlation between ad libitum feed intake and 1st litter survival. The genetic correlation of first litter survival was -0.94 and -0.60 with restricted and ad libitum feed intake respectively. This indicates that a (genetically) high feed intake (capacity) during lactation is detrimental for stayability. In Chapter 3 we did not find a biological interpretation for this phenomenon. Also table 8.4 still does not give us a possible explanation either. Results of Chapter 3 were difficult to interpret since animals that did not survive the first parity had, at best, feed intake observations on the first lactation; where those who did survive had repeated observations. In Table 8.5 results of a similar analysis as performed in Chapter 3, on the same dataset, are depicted. Next to results of the entire dataset, data on feed intake of only primiparous sows were included.

For ad libitum fed sows during lactation, the image remains the same if we include only feed intake during the first lactation: a (strong) negative genetic correlation and a small but significant positive phenotypic correlation. However, the genetic correlation between restricted feed intake during the first parity and survival of the first parity turned out to be positive (although not significantly different from zero). Similar results were found by Bunter et al. (2010). They studied the relation between ad libitum feed intake during lactation and survival into later parities (Table 8.6). In all situations the phenotypic correlation was small but positive. The negative genetic correlation between feed intake during the first parity as well as during the second parity and survival became stronger in sows which reached higher parities.

The above findings supported the idea that there is an effect of feed intake in early reproductive life which accumulates in the course of life. Sows that showed a higher feed intake during lactation were less likely to be culled in that particular lactation but if sows showed a high feed intake over successive parities sows might have been more prone for culling.

Table 8.5 Genetic (r_g) and phenotypic (r_p) correlations between (*ad libitum* and restricted) feed intake during lactation and first litter survival of sows, using either only FI of gilts or all available FI records. Bold correlations differ significantly from zero (p<0.05).

		FI restricted		FI *ad libitum*	
		r_g	r_p	r_g	r_p
1st litter survival	Only 1st litter FI	+0.14	-0.04	-0.52	**+0.16**
	Entire dataset FI	**-0.94**	-0.09	**-0.60**	**+0.15**

Table 8.6 Estimates of genetic (r_g) and phenotypic (r_p) correlations between *ad libitum* sow feed intake during lactation and sow survival to later parities. Correlations significantly different from zero in bold; after Bunter et al. (2010).

Survival to farrow in later parities	Data from	FI *ad libitum*	
		r_g	r_p
Parity 2	Parity 1	0.13	**0.09**
	Parity 2	-	-
Parity 3	Parity 1	-0.14	**0.07**
	Parity 2	**-0.74**	**0.13**
Parity 4	Parity 1	-0.50	**0.06**
	Parity 2	**-0.96**	**0.06**
Parity 5	Parity 1	-0.35	**0.05**
	Parity 2	**-0.74**	**0.04**

The mechanism behind this phenomenon remains unclear though. According to the study of Bunter et al. (2010) sows with higher genetic potential for lactation feed intake were larger and leaner. Higher sow weights were beneficial in early parities. But they were increasingly less beneficial in later parities where the nutritional demands of prolific and heavier sows were less likely to be met by intake (Bunter et al., 2010). Also in our study genetically heavier sows at start of lactation showed a higher first litter survival. But contrary to the study of Bunter et al. (2010) high feed intake during lactation (ad libitum and restricted) was not noted in sows that were heavier at start of lactation (neither phenotypic nor genetically). So a cumulative effect of feed intake on weight and via weight on a higher culling rate for (for example) leg weakness is less likely according to our study.

There are some negative effects known of high lactation feed intake. A high feed intake during lactation increases the risks on lactation estrus. Lactation estrus especially at the end of lactation causes a prolonged interval weaning to estrus and thus a higher chance for culling. No studies on lactation estrus were found but some sow crosses may be more susceptible to lactation estrus than others (M. Westerhof, TOPIGS, Vught , The Netherlands, personal communication).

High feed intake during the first days of lactation might induce the occurrence of Mastitis Metritis Agalactia (MMA). MMA syndrome-complex of the periparturient sow, accompanied by milking problems, causes not only significant economic losses but also has animal welfare issues both for the sow and its piglets (Bilkei and Horn 1991). Large differences between the composition of gestation and lactation diets is considered one of the main causes. Therefore it is usually recommended to restrict feed intake during the first days of lactation, especially to support adaptation to new lactation feeds and to reduce occurrence of post partum agalactia (Neil, 1996). The occurrence of MMA-syndrome as a consequence of high feed intake periparturient at the IPG-farm, is not likely because the step up

procedure in the feeding scheme was very conservative. Detailed information on the applied feeding scheme is given in Chapter 7.

In Chapter 3 we concluded: the only possible explanation for the severe negative genetic correlation between lactation feed intake and stayability found in literature, was provided by Tolkamp and Ketelaars (1992): increased feed intake will lead to increased oxygen intake. Consumption of oxygen has damaging effects on living organisms which are supposed to accumulate in the course of life and to result in loss of vitality, aging and finally death. In this paragraph a number of possible examples passed in review of the phenomenon described by Tolkamp and Ketelaars (1992).

Milk yield

In Chapter 3 we suggested to include litter weight gain in the breeding objective for dam lines because it has a number of advantages. Litter weight gain is (genetically) favorably correlated with total number born and favorably correlated with pre-weaning mortality. High litter weight gain is associated with higher feed intake of sows and it might be associated with higher lactation efficiency. Litter weight gain would be the trait of choice for inclusion in a breeding objective, because of easiness of measuring. In this discussion chapter we used milk yield in our classification because we wanted to emphasize more on the biological mechanisms of sow's milk production. Estimation of milk yield looks more appropriate then. Milk yield was estimated from data of weight recording of piglets. The (phenotypic) correlation between milk yield and litter weight gain is high (r=0.85), as expected. The main difference with litter weight gain was that milk yield also included estimated weight gain of those piglets that ultimately died before weaning. Definitions are given in Chapter 2.

Those sows which produce a lot of milk have a higher feed intake. Despite this they mobilize more body reserves, show a significantly reduced pre-weaning mortality and their lactation efficiency is high compared to sows with a low level of milk production. These findings are in line with the phenotypic and genetic correlations of Chapter 3. No negative effects on fertility characteristics in the next parity were found. Although not significant it looked like a trend towards a decreased interval with increasing milk production. Survival of the current cycle seemed unaffected.

Table 8.7 clearly shows the milk stimuli by piglets. Sows which produced most milk had to nurse most piglets. These piglets had the highest birth weight and they appeared to be physiologically more mature (higher gestation length) and even the within litter variation was lowest in the 10% most productive sows.

Table 8.7 Sow performances (Least Squares Means) ordered and grouped according to their estimated milk yield (respectively 10, 20, 40, 20 and 10 % of the observations). Estimated milk yield is pre-corrected for genetic line, parity of the sow and lactation length.

Trait	Classification: Estimated milk yield [1]				
	10% lowest	20% low	40% average	20% high	10% highest
Estimated milk yield, MJ ME/d	40.3	47.7	54.7	60.2	65.1
Empty weight sow at farrowing, kg	228[a]	229[a]	229[a]	229[a]	230[a]
Backfat thickness at farrowing, mm	18.1[a]	18.2[a]	18.5[ab]	18.6[b]	18.6[ab]
Fat to protein ratio at farrowing	1.33[a]	1.33[a]	1.35[ab]	1.36[b]	1.35[ab]
Total number born	13.8[a]	13.7[a]	13.3[b]	13.3[b]	13.1[b]
Avg. birth weight before cross fostering, kg	1.40[a]	1.40[a]	1.44[b]	1.48[c]	1.52[d]
Number of piglets to be nursed	11.9[a]	11.9[a]	12.0[ab]	12.1[bc]	12.3[c]
Avg. birth weight after cross fostering, kg	1.30[a]	1.37[b]	1.45[c]	1.53[d]	1.60[e]
Feed intake during lactation, kg	121[a]	125[b]	128[c]	132[d]	135[e]
Adjusted weaning weight sow, kg	224[a]	218[b]	214[c]	211[d]	208[e]
Backfat thickness at weaning, mm	15.6[a]	15.3[ab]	15.0[b]	14.5[c]	14.3[c]
Fat to protein ration at weaning	1.17[ab]	1.17[a]	1.16[a]	1.14[bc]	1.13[c]
Weight loss during lactation, kg	3.9[a]	10.3[b]	15.2[c]	18.7[d]	22.1[e]
Fat loss during lactation, kg	5.2[a]	6.5[b]	8.1[c]	9.4[d]	10.2[e]
Protein loss during lactation, kg	-0.1[a]	0.9[b]	1.5[c]	2.0[d]	2.5[e]
Pre-weaning mortality, %	20.8[a]	13.9[b]	10.6[c]	8.1[d]	6.0[e]
Number of piglets weaned	9.1[a]	10.1[b]	10.6[c]	11.0[d]	11.5[e]
Litter weight gain, kg	44.6[a]	54.8[b]	63.8[c]	71.4[d]	79.0[e]
Lactation efficiency, %	68[a]	73[b]	75[c]	77[d]	79[d]
Survival current cycle, %	76[a]	81[b]	84[bc]	85[c]	80[ab]
Prolonged interval weaning-estrus, %	11.2[a]	10.6[a]	8.2[a]	7.6[a]	7.6[a]

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

A mixed model equation (PROC MIXED SAS) demonstrated that variation in the average birth weight of piglets between litters accounted for 18% of the phenotypic variation in milk yield of the sow. The number of piglets a sows had to nurse, accounted for 2%, gestation length for almost 1.5% and within litter STD in birth weight accounted for 0.1%. Milk yield of sows is not determined by the genetic merit of the piglet for feed intake, daily gain or back fat thickness, indicating that there is no confounding between birth weight and genetic merit for the most common growing-finishing characteristics while analyzing milk stimuli by piglets. The full statistical model is given in the text box below (Box 8.2).

The effect of number of piglets to be nursed and the effect of birth weight of piglets on the estimated milk yield of the sow is depicted in Figure 8.2 and Figure 8.3 respectively.

Milk stimulus: Number of piglets to be nursed
The high milk yield with a high number of piglets to be nursed may result from a high number of functional glands. This phenomenon is confirmed by various authors (King et al., 1989; Auldist et al., 1998; Kim et al., 1999). The effect of the number of piglets on milk yield in sows reached a maximum. According to Figure 8.2 this maximum was reached when nursing 12 piglets per litter. As litter size increases from 6 to 12 piglets, milk yield increases by 56% in our dataset.

Milk stimulus: within litter Standard Deviation in piglet's birth weight
The first five pairs of mammary glands are superior to the remaining glands in milk production (Kim et al., 2000). Piglets develop a rather rigid teat order shortly after birth with highest birth-weight piglets suckling the anterior glands (Fraser and Morley Jones, 1975). Although of minor importance, the advantage of litters with reduced within litter STD in birth weight might be caused by heavier piglets suckling the posterior glands and thus providing an extra stimulus for the least productive glands. The relationship between within litter STD of birth weight and milk yield is linear, as is the relationship between gestation length and milk yield.

Milk stimulus: Birth weight
Piglet's birth weight is by far the most important milk stimulus. Heavy piglets may empty sows glands more completely than light piglets and thus minimizing the extent of down regulation of milk synthesis due to incomplete milk removal (King, 2000). Large piglets may massage the teat more vigorously before milk ejection, thus achieving a greater production per gland. The nursing frequency of heavier piglets may be higher than lighter piglets. Secretion of milk that is available to the piglet is almost complete within 35 minutes after the preceding nursing bout (Spinka et al., 1997). Thus, piglets suckling more frequently will drink this standard dose more frequently and hence have a higher total milk intake. It also means that a high nursing frequency may be beneficial for milk output. Irrespective of the biological background, increased total milk yield in response to heavier piglets is associated with increased production per gland (Auldist et al., 2000).
Van der Steen and De Groot (1992) studied the breed effects in Meishan and Dutch breeds on milk intake and growth of piglets during lactation. Meishan as well as Dutch sows nursed mixed litters of Meishan and Dutch piglets. Average birth
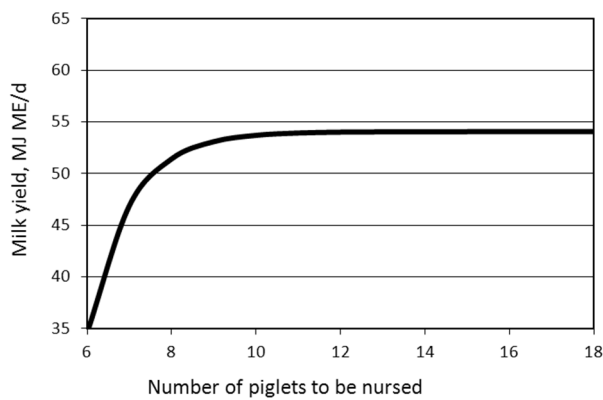
Figure 8.2 Milk stimulus: Number of piglets to be nursed

weight of Dutch and Meishan piglets was 1,354 and 885 g respectively. At an average birth weight difference, growth rate from birth to 21days was 25% higher for Dutch than for Meishan piglets respectively. At a zero birth weight difference, the difference between the two piglet types was absent. This means that light Dutch and heavy Meishan piglets, which have an equal birth weight, have the same growth rate up to weaning. No differences between Dutch and Meishan sows for milk yields were found. However due to higher birth weights the milk intake of Dutch piglets compared to Meishan piglets was 38% higher at day 13 of lactation. According to Figure 8.3, birth weights of 885 g yields 45.2 MJ ME milk per day of lactation. Birth weights of 1354 g yields 52.9 MJ ME/day, an increase of 17% over the entire lactation, which is in line with the 25% increase in growth rate over the 21 day lactation of Dutch compared to Meishan piglets.
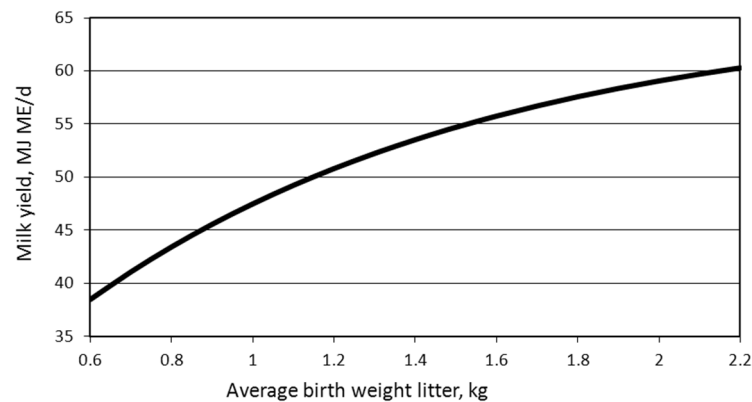
Figure 8.3 Milk stimulus: Birth weight piglets

The effect of birth weight on milk yield is becoming smaller towards high birth weights, but even in litters with an average birth weight of piglets of 2.2 kg ($\overline{x} + 3\sigma$), it appeared that milk yield had not reached its maximum (Figure 8.3).

Looking at the consequences of weight losses of sows we postulated that the driving force behind body tissue mobilization is the fat to protein ratio in the sow's body at weaning. If so, fat to protein ratio at weaning is under pressure for high milk yield sows.

Box 8.2 Statistical analyses milk stimuli by piglets.

From a biological point of view, one might expect that the effect of number of piglets to be nursed and piglet's birth weight becomes smaller towards a higher number or weight (diminishing returns-type). Therefore, birth weight (bw) and number of piglets to be nursed (tbn) were transformed, applying an asymptotic curve.

$$bw' = \frac{1}{e^{bw}} \text{ and } tbn' = \frac{1}{e^{tbn}}$$

Milk yield of sows is estimated upon weight (gain) of piglets. Piglet's birth weight might be confounded with its genetic potential for e.g. daily gain. To try to disentangle genetic merit for daily gain and birth weight of piglets, both were included in the statistical model for milk yield. The EBVs used were those based on the pedigree. Thus, own performance of the piglet was not included in the EBVs in any way.

The genetic line of the piglet might affect milk yield of the sow as well. In case of cross fostering with different genotypes present, potentially sows have to nurse different genotype piglets. Estimation of the effect of the genetic line of the piglet becomes challenging then.

While estimating breeding values, the genetic line of an animal was omitted in the statistical model. In this way genetic merit represents the additive genetic effect plus the effect of the (genetic) line. At the research farm of Beilen 25% of the live born piglets were cross fostered. At every moment four different genotypes are present (two sow crosses sired by two sire lines). As a consequence, most sows nurse different genotype piglets. Using EBVs with the effect of the genetic line included automatically takes care of the effect of the genetic line of the piglet(s).

Analyses were performed using PROC MIXED in SAS/STAT software (SAS, 1999). The full model becomes:

$$Milk\ yield = \mu + b_1 \times bw' + b_2 \times tbn' + b_3 \times GLE + b_4 \times STD_{bw} + b_5 \times EBV_{dg} + b_6 \times EBV_{fi} + b_7 \times EBV_{bf} + b_8 \times LLE + PARITY + \underline{HYS} + \underline{SOW} + e$$

where: μ = population mean; GLE = Gestation length, d; STD$_{bw}$ = Standard deviation birth weight , g; EBV = Estimated Breeding Value (for daily gain (dg), feed intake (fi) and Ultrasonic back fat (bf) respectively); LLE = Lactation Length, d; PARITY = the parity of the sow, parity six and higher were combined; HYS = Herd-Year-Season = three weeks batch of farrowing (random); SOW=the (random) effect of the sow. The random effect of the sow also takes into account the effect of the genetic line of the sow; e = residual.

None of the EBVs appeared to affect milk yield of sows significantly. Therefore, the effects were omitted in the final model.

Is milk production the driving force behind feed intake?

The control of feed intake and regulation of energy mobilization is extremely complex and are influenced by a large number of factors. Voluntary feed intake is regulated at two levels (Revell and Williams, 1993). The first is short-term regulation, which involves the factors regulating meal eating behavior, i.e. meal size and meal length. The second is long-term regulation, which determines the average daily intake over a period of time. Signals from the gastrointestinal tract and also levels of some hormones are of major importance in the short-term control of voluntary feed intake. Metabolic factors are likely to be more important for long-term control.

The physiological drive of lactating sows to produce milk at the expense of other body functions is a key component of the metabolic state of lactating sows. Therefore, it is not unlikely that milk production is the ultimate drive for the appetite to consume high amounts of feed. Milk production on its turn is primarily affected by the nursing demand of the sucking pigs during lactation (King 2000). Hence it appears that the nursing stimulus of piglets affects feed intake of sows. In Table 8.8 sow performance depending on the average birth weight after cross fostering is depicted.

Average birth weight of piglets to be nursed

It looks like high birth-weight piglets stimulate sows to produce the maximum amount of milk. The maximum milk production of these sows might be close to their physiological limits judging after the performance during their next cycle. The number of piglets per first insemination resulting from multiplication of farrowing rate and total number born, was significantly reduced in the highest birth weight class, culling (opposite of survival next cycle) was highest. This was unexpected since milk yield of the 10% highest class of Table 8.8 was lower compared to the highest class of Table 8.7. The sows of 10 % highest class based on milk yield (Table 8.7) did not demonstrate a reduced fertility in the next cycle.

Data in Table 8.8 show hardly any difference in sows at start of lactation (weight, fat to protein ratio, % stillborn) between those that had to nurse heavy and those that nursed light piglets, except the litter size. Litter size was significantly lower in sows that had to nurse the heaviest piglets. As a consequence, average birth weight was highest of these sows. Heavy piglets at birth were probably the predestination of forming litters with heavy piglets by cross fostering and thus nursing heavy piglets.

The most striking figures in the table above are those for feed intake. The 10% sows that were stimulated most by their piglets to produce milk do so at the cost of body

Table 8.8 Sow performances (Least Squares Means) ordered and grouped according to the average birth weight of their piglets after cross fostering (respectively 10, 20, 40, 20 and 10 % of the observations). Average birth weight is pre-corrected for genetic line and parity of the sow.

Trait	Classification: Average birth weight after cross fostering [1]				
	10% lowest	*20% low*	*40% average*	*20% high*	*10% highest*
Average birth weight, kg	1.02	1.22	1.45	1.65	1.86
Empty weight sow at farrowing, kg	228[a]	228[a]	229[a]	230[ab]	232[b]
Backfat thickness at farrowing, mm	18.2[a]	18.2[a]	18.4[a]	18.5[a]	18.6[a]
Fat to protein ratio at farrowing	1.33[a]	1.34[a]	1.35[a]	1.36[a]	1.35[a]
Total number born	14.5[a]	14.8[a]	13.7[b]	12.4[c]	10.6[d]
Avg. birth weight before cross fostering, kg	1.28[a]	1.30[b]	1.42[c]	1.57[d]	1.76[e]
Number of piglets to be nursed	13.1[a]	12.4[b]	11.9[c]	11.6[d]	11.3[e]
Feed intake during lactation, kg	129[ac]	126[b]	129[c]	127[ab]	129[ac]
Adjusted weaning weight sow, kg	220[a]	217[b]	214[c]	211[d]	210[d]
Backfat thickness at weaning, mm	15.4[a]	15.1[ab]	14.9[bc]	14.7[c]	14.6[c]
Fat to protein ratio at weaning	1.17[a]	1.16[ab]	1.15[ab]	1.15[b]	1.15[ab]
Weight loss during lactation, kg	7.8[a]	11.6[b]	14.6[c]	18.5[d]	21.0[e]
Fat loss during lactation, kg	6.0[a]	7.1[b]	8.1[c]	9.3[d]	9.5[d]
Protein loss during lactation, kg	0.5[a]	1.0[b]	1.4[c]	2.0[d]	2.4[e]
Pre-weaning mortality, %	20.8[a]	15.6[b]	10.4[c]	6.7[d]	5.1[d]
Number of piglets weaned	10.1[a]	10.3[b]	10.5[c]	10.7[de]	10.7[ce]
Milk yield, MJ ME/d	48.4[a]	50.8[b]	54.4[c]	56.5[d]	57.8[e]
Lactation efficiency, %	73[a]	75[a]	75[b]	76[b]	76[b]
Survival current cycle, %	85[a]	80[b]	84[a]	83[ab]	79[b]
Prolonged interval weaning-estrus, %	9.6[ab]	8.2[ab]	7.2[a]	11.5[b]	10.3[ab]
Number of piglets per 1st insemination	12.9[ab]	13.0[a]	12.6[ab]	12.3[b]	11.5[c]

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

reserves. Feed intake was not affected. Revell and Williams (1993) suggested that a negative energy balance because of the high milk production is responsible for high feed intake on the long term. This phenomenon was also used as explanation for the relatively low genetic correlation between feed intake as a grower-finisher and as a lactating sow as found in Chapter 6.

Sows that are genetically capable of producing high quantities of milk can be stimulated by piglets to do so. Feed allowance (perhaps also voluntary feed intake) is limited during the first days after farrowing. At that stage, milk production goes at the cost of body reserves. From a certain moment onwards feed intake begins to play a role. Although piglets seem to stimulate a sow to produce milk and piglets seem not to affect feed intake of the sow, it still might be the case that milk

production itself determines the long term control of feed intake. A separate analysis showed that birth weight of the piglets, birth weight variation and gestation length did not significantly affect feed intake of the sow (results not shown). Only the number of piglets was significant, probably by affecting the number of functional glands.

It might be that piglets determine the speed with which sows reach their genetic potential milk production. Once sows have reached their maximum milk production, piglets do not play a role anymore in stimulating the sow, other than affecting the number of functional glands. King et al. (1997) found an increase in milk yield of 20% or more during the initial week of lactation when fostering 2-wk-old piglets onto newly farrowed sows, although at midlactation, milk yield was not different from controls. The suggestions that only the piglets affect milk yield in early lactation could not be confirmed in our dataset since no observations of piglet's weights (and thus milk yield) during the course of lactation were available.

Colostrum intake

Colostrum production is a very critical part of the milk production of sows. Piglets are born with a limited amount of energy reserves and devoid of immune protection. Intake of colostrum, which provides both energy and maternal antibodies that protect the piglets until their own immune system matures, is of the utmost importance for survival. However, competition among siblings of variable birth weight for access to colostrum is intense and failure to achieve a regular and sufficient intake of colostrum is a major cause underlying production losses (le Dividich et al., 2005).

The average colostrum consumption is 210 to 280 g/kg of piglet over the first 24 hours of life (Le Dividich et al., 2005). However, the within-litter colostrum consumption is highly variable. When colostral access is unlimited, the ingestive capacity is much higher (approximately 450 g/kg BW; Le Dividich et al., 2005). The energy requirement is met by the consumption of 160 to 170g colostrum / kg birth weight (220 to 250 g for a 1.4 kg piglet). The acquisition of insufficient passive immunity is unlikely to be a major factor underlying early mortality of piglets (Le Dividich et al., 2005).

Gestation length has been shown to be a stimulus for milk yield (see section 'Milk yield'). The effect of gestation length could be allotted to a higher maturity of piglets, and thus have been a characteristic of the piglet. Milon et al., (1983) showed that premature farrowing (110-111 days) reduces colostrum production by 40%. A reduced colostrum production is also observed after induction of parturition, which supports the observation of Milon et al. (1983). The effect of

gestation length on milk yield can as well be a characteristic of the sow. According to Le Dividich et al. (2005) colostrum production by the sow is largely independent of litter characteristics such as litter size. The sow herself accounts for 65% of variability in litter weight gain in the first 24 hours after parturition and thus of colostrum production. Finally, milk type ewes produce significantly more colostrum than meat-type ewes (Pattinson and Thomas 2004), suggesting that the ability to produce colostrum has a genetic component.

At this early stage of lactation, the impact of udder stimulation by piglets is not likely a factor yet and most of the colostrum is consumed within a few hours following parturition. A low colostrum yield may therefore be mainly attributed to a poor ability of the sow to produce colostrum, making the supply inadequate to meet the piglet's needs. Either failure to produce or a low yield of colostrum might be caused by the occurrence of Metritis, Mastitis and Agalactia syndrome, a common disorder in periparturient sows.

Summary
Commercial pork producers have developed strategies to ensure high feed intakes during lactation to meet the energy and nutrients requirements of the sow for milk production and maintenance. However, there may be scope to further increase milk yield of well-fed sows by paying attention to factors apart from nutritional management. Sow milk yield is primarily affected by the nursing demand of the sucking pigs during lactation. Results from various studies have demonstrated that increasing nursing stimulus, whether it is through increased litter size, litter weight, or nursing frequency, increases the daily milk yield of sows. Nursing frequency and the completeness of milk gland emptying play crucial roles in level of milk output. Thus, any management or husbandry factor that lead to shorter nursing intervals or more complete removal of milk from the udder will increase sow milk yield and milk intake by the pigs. Consequently, weaning weight will increase.

At the start of lactation full udder stimulation by piglets is not likely to take place yet. A low colostrum yield may therefore be mainly attributed to a poor ability of the sow to produce colostrum. Either failure to produce or a low yield of colostrum might be caused by the occurrence of Metritis, Mastitis and Agalactia syndrome. The acquisition of insufficient passive immunity is unlikely to be a major factor underlying early mortality of piglets in healthy sows.

Lactation efficiency
In the general introduction we raised the possibility of selection for lactation efficiency as one of the measures to overcome the apparent contradiction in

selection direction for low feed intake during growing finishing and a high lactation intake. In Chapter 3 we demonstrated that the genetic correlation between lactation efficiency and feed intake was negative (r_g=-0.38 and -0.74 with ad libitum and restricted feed intake during lactation respectively). From these genetic correlations it was concluded that selection for lactation feed efficiency should be accompanied by selection for feed intake. In Chapter 6 it was demonstrated that the genetic correlation between feed efficiency during growing-finishing and lactation is high (r_g=+0.51). Selection for feed efficiency in grower-finishers will therefore most probably also lead to increased feed efficiency during lactation. Increased lactation efficiency is economically important in itself. Despite reduced feed intake during lactation, improved lactation efficiency is worthwhile achieving. Therefore, the consequences of (phenotypic) selection for lactation efficiency are depicted in Table 8.9.

(Energy) Efficient sows were leaner at start of lactation judged from their fat to protein ratio at farrowing. Generally it is expected that lean animals are the most efficient animals. Lean grower-finishers for example showed a reduced residual feed intake and were thus most efficient (Chapter 6). Viewed in that light the slightly positive genetic correlation between fat mass at the start of lactation and lactation efficiency (Chapter 6: r_g=+0.05; non significant) was unexpected.

Feed intake and fat mobilization was reduced in efficient sows. Protein mobilization however was higher. Variation in feed efficiency is mainly caused by variation in maintenance requirements of animals with similar production and body weight (De Haer et al., 1993; Luiting et al., 1994). Reduction in maintenance requirements will reduce energy requirement rather than protein requirement (NRC, 1988). Feed intake of efficient sows was apparently not high enough to provide the protein needed for milk synthesis. Therefore efficient sows need to mobilize protein from body tissue in such a quantity that at weaning the fat to protein ratio was higher in efficient sows compared to less efficient sows. If the dietary protein supply during subsequent gestation was insufficient to compensate for the shortcoming of the previous lactation, this becomes an important negative factor for the sows with the highest protein mobilization. In Chapter 2 we formulated the hypothesis that "Efficient sows may not waste energy in extra activity". In that case, there is extra energy available for the production of milk (energy requirement for maintenance is overestimated). The low activity of sows is likely to be favorable for pre-weaning survival of piglets." The behavioral study of Chapter 4 confirmed the supposition of lower activity in higher lactation efficient sows. High milk yield and reduced pre-weaning mortality in energy efficient sows can indeed be seen in Table 8.9.

Table 8.9 Sow performances (Least Squares Means) ordered and grouped according to their lactation efficiency (respectively 10, 20, 40, 20 and 10 % of the observations). Lactation efficiency is pre-corrected for genetic line, parity of the sow, Herd Year Season of the litter and lactation length.

Trait	Classification: Lactation efficiency [1]				
	10% *lowest*	*20%* *low*	*40%* *average*	*20%* *high*	*10%* *highest*
Lactation efficiency, %	60	66	71	81	97
Empty weight sow at farrowing, kg	231[bc]	227[a]	229[b]	229[ab]	233[c]
Backfat thickness at farrowing, mm	19.2[a]	18.3[b]	18.1[b]	17.7[c]	17.6[c]
Fat to protein ratio at farrowing	1.39[a]	1.34[b]	1.32[c]	1.30[d]	1.28[d]
Total number born	13.9[a]	13.2[bc]	13.4[ab]	13.0[c]	13.5[abc]
Avg. birth weight before cross fostering, kg	1.39[a]	1.44[bc]	1.44[bc]	1.45[c]	1.40[ab]
Number of piglets to be nursed	11.5[a]	11.8[ab]	11.9[b]	12.0[bc]	12.2[c]
Avg. birth weight after cross fostering, kg	1.36[a]	1.43[b]	1.44[b]	1.46[b]	1.44[b]
Feed intake during lactation, kg	134[a]	134[a]	131[b]	125[c]	117[d]
Adjusted weaning weight sow, kg	217[bc]	215[a]	216[ab]	216[ab]	220[c]
Backfat thickness at weaning, mm	14.3[a]	14.4[a]	14.9[b]	15.1[b]	15.8[c]
Fat to protein ratio at weaning	1.10[a]	1.12[a]	1.14[b]	1.16[c]	1.20[d]
Weight loss during lactation, kg	14.0[a]	13.4[a]	14.1[a]	13.2[a]	12.5[a]
Fat loss during lactation, kg	10.3[a]	8.8[b]	7.7[c]	6.3[d]	4.6[e]
Protein loss during lactation, kg	0.9[a]	1.1[a]	1.4[b]	1.4[b]	1.6[b]
Pre-weaning mortality, %	13.6[b]	12.8[ab]	11.2[a]	11.7[ab]	14.0[b]
Number of piglets weaned	9.8[a]	10.2[b]	10.4[c]	10.4[c]	10.4[c]
Milk yield, MJ ME/d	47.5[a]	51.4[b]	54.4[c]	55.3[d]	54.8[cd]
Survival current cycle, %	82[ab]	87[a]	84[a]	85[a]	79[b]
Prolonged interval weaning-estrus, %	11.4[a]	9.6[a]	7.3[a]	9.7[a]	6.6[a]

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

Nevertheless, the increment is not present from the 20% high efficient sows to the 10% most efficient sows. The question arises if limited feed intake of the 10% most efficient sows limits further milk production improvement and also if it further reduces pre-weaning mortality improvement? If these questions are replied in the affirmative it supports the idea that selection for feed efficiency should be accompanied by selection for feed intake.

Conclusions

In this section, consequences of unilateral (phenotypic) selection are shown. The fear for impaired fertility of a cycle following a lactation with high weight loss could not be confirmed. The two major causes of impaired fertility: Impaired LH levels during lactation and impaired follicle development during (and after) lactation, might be less dependent on the energy balance during lactation as a consequence

of genetic selection for decreased interval weaning to estrus, litter size and stayability. Nevertheless, it is still possible that good farm management prevented the negative effects to take effect, even if these management measures remain unknown.

Genetic selection for lean and efficient grower-finishers will increase leanness of sows (Chapter 6). The low genetic correlation between feed intake as a grower-finisher and as a lactating sow already disproved that selection for lean and efficient grower-finishers was one of the major causes for increased negative energy balance during lactation. Fatness at the start of lactation does not affect fertility or prolificacy in the next cycle. Lean sows compensate their inability to mobilize fat stores by a higher feed intake and higher feed efficiency. A high susceptibility (less robustness) of lean sows can not be ruled out.

The latter conclusion raises the question whether consequences of selection do reach the physiological limits of sows. This section demonstrated that there is no reason to expect reaching of this physiological limit to piglet production on the long run (at least five years in the perspective of the analyses performed). Nevertheless, in extreme situations some risks may become visible. (i) Unlimited selection for lactation efficiency reduces feed intake, and as a consequence protein intake, to such extend that milk production of sows is impaired. An increased protein level in the lactation or gestation diets or both is a short term solution. (ii) Data of sows which show a high feed intake during lactation suggest that piglet production was uncomplicated during and after high feed intake lactation. Sows become less energy efficient though, thus increasing the ecological footprint of pig production. Besides, genetic selection for increased feed intake during lactation will reduce the stayability of sows. This indicate a physiological limit, although, this phenomenon is not yet fully understood. (iii) High milk yields of sows facilitate high piglet production. It also reduces pre-weaning mortality of piglets. High birth weight of piglets is by far the most important stimulus for milk production of the sow during early lactation. If we force sows to nurse piglets with a high birth weight without sufficient milk production capacity it may impair sow's fertility during the next parity. And this points to a physiological limit.

High milk production in itself does not show any negative side effects. This leads to the conclusion that selection for higher birth weight should be accompanied by, at least, selection for increased milk yield. In general, unilateral selection should be avoided and the aim should be for balanced genetic selection to prevent possible negative side effects. In the next section an example of a balanced breeding objective along with a few alternative ones will be shown.

The example of the apparent protein deficiency of high energy efficient sows, demonstrates that next to breeding strategies, environment or husbandry should keep pace with increased piglet production as well.

8.3 Comparison of alternative breeding programs

A breeding program aims at improving a combination of traits which is referred to as the breeding objective. In the breeding objective, the different traits are given an economic weight which reflects the desired direction of change and the relative importance of the trait. In this section, consequences of changes in economic weights and in traits are evaluated for a dam line. To predict the consequences of multitrait selection the simulation program MTINDEX was used (Van der Werf, 2005). Animals were assumed to be selected on an index (I) which equals their expected value for the breeding objective which mimics the situation in practice. The following aggregate genotype was used:

$$H = EW_{trait_1} \times BV_{trait_1} + EW_{trait_2} \times BV_{trait_2} + \cdots \ldots \ldots + EW_{trait_n} \times BV_{trait_n},$$

where EW is the 'Economic Weight' and BV the 'Breeding Value' for a trait in the breeding objective. To predict the consequences of multitrait selection, a selection index was used. The formula for the index (I) is identical to the formula for the aggregate genotype where the BV of the aggregate genotype was replaced by the Estimated Breeding Value (EBV).The Economic weight is the marginal economic values as derived by Hanenberg et al. (2010). The marginal economic value of the traits is calculated as change in predicted profit, holding all other traits constant. Detailed information on the simulated breeding program is given in Box 8.3. Genetic gain was simulated for five dam-line breeding objectives:

1. A 'traditional' breeding objective with emphasize on fertility and grower-finisher characteristics;

And four alternative breeding objectives with next to the traditional breeding objective attention for

2. Feed intake during lactation;
3. Milk yield;
4. Average piglet's birth weight;
5. Lactation efficiency.

Prediction of the selection response requires knowledge of genetic correlations between traits in the index. Genetic correlations between fertility traits and lactation performance traits were taken from Chapter 3 and between grower-

Box 8.3 Breeding program used for simulation in section 8.3

To model the breeding program, the following assumptions were made:
- An active population of 5 000 sows, with an annual replacement of 40%;
- 50 sires were used every year;
- 15% of the litters produced were purebred litters for which on average third parity sows were used;
- Each sow produced 2.4 litters per year;
- Per purebred litter 3.33 female piglets and 1.66 male piglets were performance tested;
- Single-stage-selection was simulated separately for sires and dams:
  1. (1250) Boars were performance tested. On test and off test weight was recorded along with feed intake during test. At the end of the performance test backfat thickness and loin depth was recorded;

     At the end of the performance test BLUP-EBV selection for young boars was performed. At that moment information on total number born, percentage still born, pre-weaning mortality, percentage prolonged interval weaning to estrus on 4 litters of the mother was available;

     Sires produce offspring during 0.5 year (10-16 months of age) resulting in a generation interval of 13 months;

     At the end of the performance test, information of the performance test of the father, the mother, the animal itself, 4 full sibs and 70 half sibs were included in the BLUP-EBV. For feed intake (only recorded on males) information on the father, the animal itself, 0.67 full sibs and 23.3 half sibs was available.
  2. (2500) Gilts were performance tested. On test and off test weight was recorded. At the end of the performance test backfat thickness and loin depth was recorded. Sows were introduced in the sow herd and were selected based on BLUP-EBV to produce a purebred litter (or not).

     At that moment information on total number born, percentage still born, pre-weaning mortality, percentage prolonged interval weaning to estrus and 1st litter survival is available on 2 litters of the sows herself, on 7 litters of full sibs and 140 litters of half sibs along with 6 litters of the mother.

     The generation interval for via the dam-side was assumed to be22months;

     At the end of the performance test, information of the performance test of the father, the mother, the animal itself, 4 full sibs and 70 half sibs were included in the BLUP-EBV. For feed intake information on the father, 1.67 full sibs and 23.3 half sibs was available.
- Piglets that were not performance tested were excluded for reasons other than the breeding objective;
- 12% of the performance tested males were potentially available for reproduction, yielding a selection intensity of 1.08. All other boars (88%) were excluded for reasons other than the breeding objective;
- 75% of the first litter sows produced a third litter. The remaining 25% were excluded for reasons other than the breeding objective. The selection intensity via the female side was assumed to be 0.97.

Phenotypic variances and heritabilities needed in MTINDEX were obtained from Chapter 3 and Chapter 6. Neither of the chapters contains co variances between fertility traits and grower-finisher traits. Both datasets were combined to estimate the remaining genetic parameters needed for the simulation. In this section (8.3) we made a distinction between ad lib feed

> **Box 8.3** Breeding program used for simulation in section 8.3 (continued)
>
> intake and restricted feed intake of sows during lactation. In Chapter 6, both traits were treated as one. However, the genetic correlation estimates were based on the same dataset. Presented heritabilities and genetic correlations in Table 8.10 can differ slightly from those presented in Chapter 3 or Chapter 6. The genetic parameters depicted in Table 8.10 are those after bending to make the variance-covariance matrix positive definite.

finisher traits and lactation performance traits from Chapter 6. To be able to mimic a breeding objective as used in day to day practice, the genetic correlations between fertility and grower-finisher were estimated from the combined dataset of Chapter 3 and 6 (see Table 8.10).

In simulating the response to selection, genetic parameters of % prolonged interval after weaning and stayability first litter were based on the observed scale rather than on the underlying distribution, because of easier interpretation of the results. With a threshold model heritabilities are estimated on the assumed underlying scale. These estimates are expected to be higher than heritabilities estimated on the observed scale (Dempster and Lerner, 1950). The heritability, based on the underlying distribution is 0.30 for both traits (results not shown). In the simulations, a heritability on the binary scale was used (0.08 and 0.05 for % prolonged interval after weaning and stayability first litter respectively).

In the traditional breeding objective for dam lines, fertility traits and grower-finisher characteristics are weighed according to their economic value. Sows account for 50% of the grower-finisher offspring. Therefore, the economic value for grower-finishers traits in the dam lines has to be multiplied by 0.5. The genetic consequences of the traditional breeding program are depicted in Table 8.11. In the traditional breeding program no economic weight is assigned to lactation performance traits. The genetic response in lactation performance traits in Table 8.11 is the result of a correlated response due to selection on traits with an economic weight. Also average birth weight has no economic value. The added value of birth weight shows via reduced mortality and/or improved grower-finisher characteristics. Residual feed intake does not have an economic value either since feed intake already has a (negative) economic value.

The traditional breeding objective yields favorable changes for all traits with a non-zero economic value in the breeding objective, except for feed intake of grower-finishers. Using the average performance of the IPG-farm over 2009 (Table A8.1), the expected increase in number of piglets weaned per litter will be 0.22 per year.

Table 8.10 Heritabilities (diagonal) and genetic correlations (below the diagonal) between traits measured on sows used in the simulation of consequences of different breeding objectives.

	Trait	Fertility						Lactation performance							Growing-finishing				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Fertility	1 Total number piglets born	0.13																	
	2 Average birth weight, g	-0.39	0.35																
	3 Percentage still born, %	0.44	0.07	0.10															
	4 Pre-weaning mortality, %	0.34	-0.27	0.10	0.06														
	5 Prol. interval w - 1st ins, %	-0.07	0.01	-0.04	0.09	0.08													
	6 1st litter survival, %	0.02	0.04	-0.17	-0.12	-0.12	0.05												
Lactation performance	7 Weight sow, kg	-0.10	-0.10	0.15	-0.09	0.23	0.45	0.45											
	8 Fat mass sow, kg	-0.23	-0.20	0.01	-0.13	0.19	0.30	0.64	0.52										
	9 Weight loss sow, kg	0.03	0.24	0.04	-0.10	0.02	0.29	-0.26	-0.21	0.20									
	10 Ad lib lactation FI, kg	0.01	0.02	-0.05	-0.06	0.16	-0.56	0.07	0.12	-0.59	0.30								
	11 Restricted lactation FI, kg	0.01	0.02	-0.04	-0.38	-0.16	-0.62	-0.32	-0.14	-0.18	0.57	0.14							
	12 Litter weight gain, kg	0.34	0.27	0.15	-0.36	0.18	-0.11	-0.08	-0.21	0.23	0.37	0.30	0.18						
	13 Lactation efficiency, %	0.12	-0.03	0.13	-0.18	0.09	0.34	0.24	-0.06	0.08	-0.31	-0.57	0.18	0.12					
Growing Finishing	14 Daily gain, g/d	-0.06	0.45	-0.06	-0.34	0.00	0.01	0.25	0.05	-0.10	0.36	0.29	0.14	-0.13	0.24				
	15 Ultrasonic backfat, mm	-0.01	-0.26	0.05	0.16	-0.03	-0.23	-0.01	0.54	-0.43	0.36	-0.05	-0.26	-0.06	0.01	0.37			
	16 HGP loin depth, mm	-0.06	-0.11	-0.33	0.03	0.02	0.01	-0.16	-0.17	0.12	-0.35	-0.08	-0.09	-0.12	-0.07	-0.11	0.24		
	17 Feed intake, kg/d	0.05	0.11	-0.12	-0.25	0.07	0.07	0.19	0.23	-0.23	0.45	0.25	0.02	-0.28	0.78	0.29	-0.19	0.19	
	18 Residual feed intake, g/d	-0.08	0.12	0.05	-0.14	0.09	0.00	-0.06	-0.31	0.31	0.05	0.23	0.12	-0.40	0.12	-0.51	-0.18	0.28	0.11

The total number of piglets born is expected to increase by 0.20 per year. This suggests that the absolute number of piglets that died until weaning decreased slightly. This conclusion also holds when using the average performance data of Dutch farms in 2009 instead of the IPG farm.

The breeding objective as depicted in Table 8.11 yields a cost price reduction per slaughter pig produced of €1.37 per year. This reduction is calculated as the sum of the yearly selection response in traits included in the breeding objective multiplied by its economic value.

Table 8.11 Additive genetic standard deviation (σ_A), economic value (EV) and selection response per gender ($r_{IH} \times \sigma_A$) and per year (ΔG/year) applying a 'traditional' breeding objective. The last column indicates whether the change is in the desired direction.

	Traits	σ_A	EV (€)[1]	Selection response				
				$r_{IH}*\sigma_A$ ♂	$r_{IH}*\sigma_A$ ♀	ΔG/ year	ΔG as % of σ_A	Desired Y/N
Fertility	Total number of piglets born	1.12	3.140	0.12	0.48	0.20	18	Y
	Average birth weight, g	0.11	-	21	-4	6	5	Y
	Percentage still born, %	3.5	-0.433	-0.3	0.0	-0.1	2	Y
	Pre-weaning mortality, %	2.8	-0.550	-0.5	-0.4	-0.3	11	Y
	Prolonged interv. w-1stins.,%	8.7	-0.014	-0.1	-1.0	-0.4	4	Y
	1st litter survival, %	8.0	0.050	1.3	1.7	1.0	13	Y
Lactation performance	Weight sow, kg	10.6	-	0.7	0.1	0.3	3	N
	Fat mass sow, kg	4.9	-	-1.3	-1.3	-0.9	18	?
	Weight loss sow, kg	5.8	-	1.1	1.0	0.7	12	N
	Ad lib feed intake, kg	10.4	-	-1.0	-1.2	-0.7	7	N
	Restricted feed intake, kg	6.7	-	0.8	0.7	0.5	8	Y
	Litter weight gain, kg	4.3	-	0.8	1.3	0.7	17	Y
	Lactation efficiency, %	3.7	-	-0.1	0.3	0.1	1	Y
Growing – finishing	Daily gain, g/d	43	0.094	15	10	9	21	Y
	Ultrasonic backfat, mm	1.20	-1.145	-0.6	-0.4	-0.4	30	Y
	HGP loin depth, mm	2.68	0.164	0.5	0.4	0.3	11	Y
	Feed intake, kg/d	115	-0.024	21	17	13	11	N
	Residual feed intake, g/d	62	-	17	8	9	14	N

[1] After Hanenberg et al. (2010)

The traditional breeding objective puts relatively much emphasis on grower-finisher characteristics since ultrasonic backfat thickness improves by 30% of the genetic standard deviation and daily gain by 21%. In contrast, litter size 'only' improves by 18% of the genetic standard deviation. The risks of such a breeding objective appeared to be the low (ad libitum) feed intake during lactation and as a consequence the increased weight loss during lactation. After ten years of selection, sows would loose an extra 7 kg body weight during lactation. Increased leanness of sows will partly compensate weight loss. Increased weight loss did not result in a higher percentage of prolonged intervals after weaning while mature weight of the sow only increased marginally. The marginal change in mature weight is somewhat unexpected since it is generally assumed that mature weight increases as production increases (Luiting et al., 1994). The accuracy of the breeding values for fertility characteristics is relatively high at selection of the females and relatively poor at selection of the males. Consequently, genetic response in fertility characteristics predominantly originates from the selection in females, while male selection contributes more to genetic response in grower-finisher characteristics. Selection of males would indeed increase mature weight. Probably because of the negative genetic correlation between litter size and weight of the sow, selection in sows has only a limited effect on weight of the sow.

The only trait in the breeding objective that changes in the undesired direction is feed intake as a grower-finisher. Increased feed intake as a grower-finisher has a negative impact on the cost price of a slaughter pig. Nevertheless, the marginal feed:gain ratio of 1.44 g/g (Δ feed intake/ Δ daily gain) is much better then the 2.50 (g/g) over the entire growing-finishing trajectory (see Table 6.1). This improved feed:gain ratio does not translate into a reduced residual feed intake which is unexpected.

As already mentioned before, weight loss of sows during lactation will increase as a consequence of the traditional breeding program. If this is perceived as undesirable for example because we can not completely overlook the consequences of ever increasing weight loss, alternative breeding objectives may be available. In Table 8.12, consequences of four alternative breeding objectives are described: an alternative where ad libitum feed intake during lactation is included in the breeding objective (Alternative 2), an alternative with litter weight gain included (Alternative 3), an alternative with average birth weight of the piglets included (Alternative 4) and finally an alternative where lactation efficiency is added to the traditional breeding objective (Alternative 5). Economic values for these traits are unknown. Therefore a desired gain was used. The objective of the alternatives was to improve the additional trait by 25% of its genetic standard deviation while keeping the

Table 8.12 Selection response per year (ΔG/year) for total breeding objective and individual traits in breeding objective resulting from five different breeding programs.

		Alternative breeding objectives				
	Breeding program	_1_	_2_	_3_	_4_	_5_
		Traditional extra obs.	_Ad libitum Feed intake_	_Litter weight gain_	_Average birth wt_	_Lactation efficiency_
	Total selection response, €/year	1.51	1.21	1.29	1.38	1.30
Fertility	Total number of piglets born	0.23	0.20	0.20	0.12	0.21
	Average birth weight, g	9	10	17	28	7
	Percentage still born, %	0.0	0.0	0.1	0.0	0.1
	Pre-weaning mortality, %	-0.4	-0.4	-0.5	-0.5	-0.3
	Prolonged interv. w-1[st]ins., %	-0.3	0.0	0.2	-0.3	-0.1
	1st litter survival, %	0.7	-0.6	0.0	0.7	1.4
Lactation performance	Weight sow, kg	-0.3	0.2	-0.5	-0.4	0.5
	Fat mass sow, kg	-1.2	-0.7	-1.1	-1.3	-1.0
	Weight loss sow, kg	0.9	-0.3	0.9	1.1	1.0
	Ad lib feed intake, kg	-0.6	2.6	0.8	-0.4	-1.5
	Restricted feed intake, kg	0.7	1.7	1.1	0.7	-0.5
	Litter weight gain, kg	1.1	1.3	1.7	1.2	1.0
	Lactation efficiency, %	0.2	-0.1	0.2	0.2	0.9
Growing finishing	Daily gain, g/d	8	14	7	12	4
	Ultrasonic backfat, mm	-0.4	-0.2	-0.3	-0.4	-0.4
	HGP loin depth, mm	0.3	-0.1	0.0	0.2	0.2
	Feed intake, kg/d	9	30	7	12	-4
	Residual feed intake, g/d	9	8	10	11	4

relative weighing of the other traits unchanged compared to the traditional breeding objective. Litter weight gain already improves by 17% applying the traditional breeding objective (Table 8.11). Bringing it to 25% would not make a large difference. Therefore, the desired gain for litter weight gain was set at 40% of the genetic standard deviation.

Including extra traits in a breeding objective requires observations for the new trait(s). Extra observations affect the accuracy of breeding values for all correlated traits. In Table 8.12 selection responses resulting from breeding program for four alternative breeding objectives are given (Alternative 2 to 5). This table also provides the selection response resulting from breeding program with traditional breeding objective but with extra observations (Alternative 1).

The total selection response expressed as cost price reduction per slaughter pig produced in € per year, is calculated in the same way as the cost price reduction of the traditional breeding objective is. This means that changes in the extra traits in

the alternative breeding objectives are not accounted for. Advantage is that values are comparable over different breeding objectives.

Adding the information on additional traits (Alternative 1) yielded a selection response of €1.51 per year. This is 14 eurocents higher (10%) compared to the traditional breeding objective from Table 8.11. The total response reduced to €1.21 per year for the breeding objective with desired gain for feed intake during lactation (Alternative 2). This is 30 eurocents less (20%) than response from the traditional breeding objective including the extra information (Table 8.12).

It is no surprise that the Alternative 2 to 5 all result in a lower total selection response which represents cost price reduction of a slaughter pig per year. Improvement of number of piglets weaned per litter is lower in every alterative as well (results not shown). Growing-finishing traits are negatively affected as well, except for the alternative with extra emphasis on average birth weight. Selection shifts from fertility traits towards growing-finishing traits applying this alternative. The alternative breeding objective with a desired gain for lactation efficiency causes a further reduction of feed intake during lactation and increases the response in stayability and feed efficiency of grower-finishers while reducing the response in daily gain. The only alternative that reduces weight loss of sows during lactation is Alternative 2 (increased ad libitum feed intake). Feed:gain ratio in this alternative is least beneficial of all alternatives (30g/d extra feed intake for 'only' 14 g/d extra daily gain). Judged on the residual feed intake of this alternative, grower-finishers are not that inefficient. Leanness of grower-finishers does not improve that much, but genetic progress shifts towards daily gain. This is the only alternative where stayability of sows decreases. The alternative with (extra) emphasis on litter weight gain (3) also improves feed intake but to a lower extend while stayability remains unchanged. From the investigated alternatives, the only alternative that reduces weight loss of sows during lactation is the alternative with desired gain for ad libitum lactation feed intake (Alternative 2).

Lactation efficiency is a linear function of feed intake, body mobilization, (milk) production and maintenance of live weight and as such it is an attractive characteristic to represent production efficiency. The phenotypic and genetic parameters of lactation efficiency can be written as a function of its composing traits. Moreover, selection indices which include the composing traits are equivalent with an index that includes lactation efficiency. Therefore definition of the term lactation efficiency may be useful to interpret variation in production efficiency, but it does not help in obtaining a better selection response than selection on the individual components alone. In fact, multiple trait genetic evaluation of component traits rather than the trait lactation efficiency itself is

likely to be more accurate as this more appropriately accommodates different models for the component traits and missing data (Van der Werf, 2004).

The component traits of lactation efficiency are predominantly feed intake and milk yield. Both traits (feed intake and milk yield) showed some advantages in the above mentioned simulations. A combination of these two traits, added to the traditional breeding objective, might overcome the negative consequences of including the traits individually (Table 8.13).

This alternative index (index_new) leads to increased feed intake during lactation while weight loss remains unchanged. Total number of piglets born increases, percentage stillborn stabilizes, pre-weaning mortality decreases. Number of piglets weaned did not benefit, which is unexpected given the previous remarks. Improvement of litter weight gain seems to level off as the index_new increases. Lactation efficiency remains unchanged. Weight of sows (at farrowing as well as at weaning) is lower for the high index sows. No negative effect on production in the next parity was found. The alternative index (index_new) yielded a total selection response of €1.13 per year (results not shown). In this selection response the increased feed intake during lactation and the increased litter weight gain were not valued. €1.13 is a 25% reduction compared to the €1.51 of the response from the traditional breeding objective including the extra information.

The top 10% sows based on the index_new had only 12 piglets to nurse. There was no need to cross foster more piglets to these sows because the farm average was only about 12 live born piglets (in all five categories the sows had to nurse about 12 piglets). In case the farm average is 13.7 live born piglets (the average of the top 10% sows), the number of piglets to be nursed will increase too. If the top 10% sows would be loaded with a higher amount of piglets to be nursed, one might expect that weight loss is higher. Therefore, actual weight loss during lactation might be underestimated in the top 10% sows based on the proposed selection index.

A balanced selection for production and reproduction traits should be accompanied by appropriate attention to health- and welfare-related traits to avoid negative side effects. Intuitively, there is an end to what an animal can handle in terms of weight loss during lactation. Reaching physiological limits because of high weight loss might reduce health- and welfare of sows. Non-intuitively, negative side effects like decreased feed intake during lactation or increased weight loss during lactation can relatively easy be accounted for by measuring the traits and including that information in selection index and assigned an economic weight or desired goal to these traits in the breeding objective.

Table 8.13 Sow performances (Least Squares Means) ordered and grouped according to their proposed selection index (respectively 10, 20, 40, 20 and 10 % of the observations). Proposed selection index is pre-corrected for genetic line and parity of the sow.

Trait	Classification: Index_new [1]				
	10% lowest	*20% low*	*40% average*	*20% high*	*10% highest*
Number of lactations	253	508	1015	508	254
Index_new (€)	-6.6	-3.7	0.0	2.4	4.9
Parity	3.3	3.2	3.1	3.3	3.7
Empty weight sow at farrowing (kg)	235^a	229^b	229^b	225^c	220^d
Backfat thickness at farrowing (mm)	19.7^a	19.0^b	18.3^c	17.7^d	16.0^e
Fat mass at farrowing (kg)	50.1^a	48.1^b	46.7^c	45.3^d	41.5^e
Protein mass at farrowing (kg)	36.0^a	35.2^{bc}	35.3^b	34.9^{cd}	34.5^d
Fat to protein ratio at farrowing	1.41^a	1.38^a	1.34^{bc}	1.31^c	1.22^d
Gestation length (d)	115.3^a	115.6^b	115.8^c	115.7^{bc}	116.1^d
Total number born	12.6^a	12.4^a	13.6^b	14.1^c	14.7^d
Stillborn (%)	6.5^a	6.3^a	5.8^a	6.2^a	6.8^a
Litter weight before cross fostering (kg)	17.1^a	17.5^a	18.7^b	19.5^c	20.7^d
Avg. birth weight before cross fost. (kg)	1.42^a	1.47^b	1.42^a	1.44^a	1.45^{ab}
STD birth weight before cross fost. (g)	289^a	296^a	294^a	297^a	293^a
Number of piglets to be nursed	12.0^{ab}	11.8^a	12.2^b	12.2^b	12.0^{ab}
Litter weight after cross fostering (kg)	16.8^a	17.2^{ab}	17.3^{ab}	17.4^b	17.4^{ab}
Avg. birth weight after cross fostering (kg)	1.42^a	1.47^b	1.43^a	1.44^{ab}	1.46^{ab}
STD birth weight after cross fostering (g)	247^a	245^a	233^{bc}	235^{ab}	222^c
Feed intake during lactation (kg)	120^a	128^b	129^{bc}	131^c	137^d
Adjusted weaning weight sow (kg)	225^a	216^b	213^c	209^d	206^d
Backfat thickness at weaning (mm)	16.6^a	15.7^b	14.7^c	14.1^d	12.7^e
Fat mass at weaning (kg)	43.1^a	40.5^b	38.4^c	36.7^d	33.7^e
Protein mass at weaning (kg)	35.2^a	34.0^b	33.8^b	33.3^c	33.2^c
Fat to protein ratio at weaning	1.24^a	1.20^b	1.15^c	1.11^d	1.02^e
Weight loss during lactation (kg)	10.7^a	13.4^b	15.5^c	16.3^c	14.3^{bc}
Fat loss during lactation (kg)	7.2^a	7.7^{ab}	8.2^{bc}	8.4^c	8.0^{abc}
Protein loss during lactation (kg)	0.8^a	1.3^b	1.6^c	1.7^c	1.4^{bc}
Input (MJ ME/d)	51.2^a	56.2^b	57.3^b	59.9^c	62.8^d
Pre-weaning mortality (%)	16.6^a	12.0^b	10.8^c	9.9^{cd}	8.7^d
Number of piglets weaned	9.7^a	10.2^b	10.8^c	10.8^c	10.8^c
Litter weight gain (kg)	54.1^a	59.8^b	64.3^c	67.4^d	68.4^d
STD weaning weight (g)	1282^a	1254^{ab}	1222^b	1204^b	1238^{ab}
Milk yield (MJ ME/d)	47.1^a	51.0^b	54.5^c	56.8^d	57.4^d
Output (MJ ME/d)	37.5^a	40.2^b	42.8^c	44.5^d	45.0^d
Lactation efficiency (%)	74^b	71^a	75^c	74^{bc}	72^{ab}
Survival current cycle (%)	80^a	80^a	82^a	81^a	90^b
Prolonged interval weaning-estrus (%)	9.1^a	11.2^a	8.9^a	7.6^a	10.7^a
Farrowing rate of 1st ins. next parity (%)	88^a	88^a	84^a	87^a	89^a
Total number born next parity	12.6^a	12.5^a	13.7^b	14.1^b	15.0^c
Number of piglets per 1st insemination	11.8^a	11.9^a	12.8^b	12.9^b	13.8^c

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

8.4 Ethical considerations

Introduction

The simulation results of a breeding program in Table 8.11 clearly demonstrate that feed intake of lactating sows will not keep pace with the increased litter weight gain and the required higher milk production which will result in an increased weight loss of sows during lactation. Sow weight loss during lactation will increase by 7 kg during the next decade from about 14 to 21 kg. Nevertheless, based on the analysis in 8.3 no negative consequences on production numbers are expected in the short term. Weight loss of sows per se is not a problem but the associated consequences might be. Feed intake capacity of sows is high enough to recover this weight loss during the subsequent gestation period. Nevertheless, the general opinion is that excessive weight loss during lactation should be avoided, especially in primiparous sows (Hoving et al., 2010). Analyses in the previous section demonstrated that alternative breeding objectives, where extra weight losses during lactation are avoided, are possible.

The associated consequences for the producers of weight loss of sows during lactation might be: (1) increased culling, (2) increased weaning to estrus interval, (3) decreased farrowing rate and/or (4) decreased litter size of the subsequent parity. It is hypothesized that by including stayability, % prolonged interval weaning to estrus and total number born in the breeding objective, these negative consequences of weight loss during lactation could be avoided (see section 'Motivation of the present research'). Selection could lead to an increased interval estrus to pregnancy or in other words a decreased farrowing rate. The aforementioned section did not show that farrowing rate was compromised. However, one could decide to include such a trait in the breeding objective as a kind of insurance premium to prevent an undesired correlated response.

In essence, the breeding program is a black-box technique: the underlying physiological processes on which selections acts are unknown. Predictions of the response resulting from a breeding program can be made based on assumptions on the underlying genetic model, genetic parameters for the traits in the population and characteristics of the breeding program. Furthermore, effects of breeding programs in the past can be assessed by analyzing the realized response to selection. The effects of the breeding program can be quantified not only for the traits included in the selection objective but also for the other traits as long as they are recorded. This offers the opportunity to validate the assumed genetic model and monitor the consequences of the breeding program. A more detailed

knowledge of biological backgrounds will offer the opportunity to better understand and anticipate undesirable side effects of selection.

The ethical considerations regarding breeding are: should breeding companies put emphasis on characteristics without a direct economic spin off to prevent possible undesirable effects of selection? Selection against weight loss during lactation will serve as an example here. The procedure for formulating arguments and conclusion are valid in a broader perspective.

Consequences of selection

Artificial selection may lead to animals that use their resources (e.g. feed intake, mobilizable body tissue, etc.) to the maximum. This means that a limited buffer is left to the animal to respond adequately to unexpected stresses and challenges (Rauw et al., 1998). This limited buffer may lead to impaired animal welfare. According to the Resource Allocation Theory (Beilharz et al., 1993) when (internal or external or both) resources are limited a compromise has to be found by the animal how to partition available resources among functions. The theory implies that there is an optimum to what can be accomplished in a given, resource limited, environment. Increasing production by genetic selection beyond this optimum will cause problems for the animal because it is not able to acquire the essential increase in resources (Beilharz, 1998). When a population is genetically driven towards high production, and thus allocating a higher proportion of resources to production functions, less resources will be left to respond adequately to other demands, like coping with (unexpected) stressors; i.e. the buffer capacity is reduced. In this situation it is most likely that traits which are not included in the breeding objective will be the first ones from which resources will be diverted towards increased production. Modification of the environment to increase the amount of resources available to an animal or reduction of environmental stress may prevent negative side effects of selection. In section 8.2 (lactation efficiency) it was shown that selection for high energy efficient sows will increase the protein requirements. Unless the protein content of the diet is increased, this indirect effect of selection could become a limiting factor.

Prunier et al. (2010) wonder whether physiological limits are close to be reached by both the mother and the offspring. On the offspring side because increased litter size is associated with increased mortality until weaning (stillborn as well as pre-weaning mortality). On the mother side recovery of weight loss during the subsequent gestation causes rapid live weight increase during gestation which might induce leg weakness. Increased litter size might induce nutritional deficits and related problems because mineral and nutrient needs to support fetal growth and milk production (Prunier et al., 2010).

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Next to the effect for the animal itself, it is for several reasons important to prevent undesirable side effects of selection (Rauw et al., 1998): (i) there is an increasing consciousness among people of the intensive nature of animal production systems and societal resistance against some production systems will increase if animal health and welfare become more at risk; (ii) veterinary costs will further increase; and (iii) if breeding programs should be altered it may take five to ten years before genetic trends in commercial livestock are really changed.

Decision support model for ethical weighing
In December 2010, the Council for Animal Matters in the Netherlands published its view on animal breeding and the use of reproduction techniques in animal husbandry (RDA, 2010). The Council for Animal Matters published a decision support model for ethical evaluation animal breeding programmes and animal reproduction techniques. In this section, this decision support model will be used to evaluate our research question: "should breeding companies include characteristics in the breeding objective, which do not contribute to a cost price reduction of the slaughter pig, to prevent possible undesired side effects of selection?" The model is given in Box 8.4.

To answer the question, eight specific questions should be considered. Six of them address the issue of legitimacy of animal breeding or the use of reproduction techniques in general. Two questions of the decision support model apply specifically to our question whether increased weight loss as a consequence of genetic selection is acceptable. These questions are those on the consequences for animal health and welfare (Question 5) and on the consequences for animal's integrity (Question 6).

The European Forum of Farm Animal Breeders published a Code of Good Practice for Farm Animal Breeding and Reproduction Organizations (EFFAB, 2010). The main objectives of the Code are: (i) to become the standard instrument for defining and maintaining good practices for farm animal breeding; and (ii) to create transparency for the public. Implementation of the Code is voluntary. At present four of the five largest pig-breeding organizations worldwide have adopted the Code or are working on adoption of the code (A.-M. Neeteson-van Nieuwenhoven, EFFAB, Oosterbeek, The Netherlands, personal communication).

(Pig) breeding companies that have implemented the Code of Good Practice, automatically addressed a number of ethical considerations as mentioned in the decision support model of the RDA. If formulation of the Code of Good Practice is

Box 8.4 Decision support model for ethical weighing (RDA, 2010); Translated from Dutch.

'Ethical weighing'

Breeding & reproduction techniques

Based on:

Societal moral
- *Intuition (e.g. animal welfare alarming)*
- *Principles (e.g. animal welfare morally important)*
- *Facts (e.g. congenital defects)*

and

Scientific knowledge

(relevant and up-to-date)

- *Animal welfare, including animal health*
- *Heritability*
- *Reproduction*
- *Breeding programs*
- *Human-animal relation*
- *Animal vs. environment*
- *Ethics (animal integrity)*

interests are weighed.

Fundamental moral question

What is appropriate in adapting animals to our own needs and interests?

Specific questions:

1. *Analysis of the status quo of the animal population concerned. Giving societal, economical and all other arguments for applying a breeding program.*
2. *What is the objective of the proposed breeding program or reproduction technique and what is its importance and necessity?*
3. *Is the breeding program or reproduction technique feasible within 10 years?*
4. *Are there reasonable alternatives to achieve the objective?*
5. *Can the breeding program or reproduction technique cause harm to the health or welfare of the animal? In this weighing not only parents stock but also potential offspring should be considered. Or does it perhaps add to improvement in these areas?*
6. *Does the breeding program or reproduction technique affect the integrity of the animal? Or does it perhaps add to improvement in that area?*
7. *Is, by applying the breeding program or reproduction technique, food safety and public health jeopardized? And if so, how are these guaranteed?*
8. *Is, by applying the breeding program or reproduction technique, biodiversity jeopardized? And if so, how is biodiversity guaranteed?*

*The **final weighing** of all aspects while answering the specific questions, should lead to an answer to the question: does the importance of the breeding program or reproduction technique weigh against the (possible) damage?*

applicable to the questions of the decision support model, the formulation of the Code of Good Practice will be used. Below, these eight questions will be answered one by one. The formulation of these eight questions is given in the middle right textbox of the decision support model as depicted in Box 8.4.

(1) What are the arguments for applying a breeding program?
Pig breeding is an economic activity. Therefore, basic economic principles apply to pig breeding companies. This means that pig breeding companies need to be competitive in order to make profit in order to survive. The products of breeding companies are genes, packed in animals, semen or embryos, and knowledge. These products contribute to a continuously decreasing cost price of saleable meat produced by farmers or integrators. To achieve this, breeding companies execute a breeding program, applying a breeding objective for the populations they are in charge of, which aims at cost price reduction. The future competitiveness of pork in the food market depends on continued genetic improvement in the efficiency of quality lean production (Clutter and Brascamp, 1998).

From the perspective of the animal these arguments sound very aloof. Recognizing the intrinsic value of an animal (having a value of their own), by defying the instrumentalization of the animals involved, is considered important in moral weighing of the use of animals for human purposes (Brom, 1999). In the future an increasing share of livestock production will probably come from industrial enterprises. This increase in scale will be accompanied by less labor available per animal (see general introduction). Nevertheless, defying instrumentalization is not only a matter of attention but mainly a matter of mentality of everybody involved in pig husbandry. Therefore, instrumentalization becomes an issue of pig husbandry rather than pig breeding and with that it is not an argument which has to be considered while weighing arguments for applying a breeding program.

(2) What is the goal of the breeding program?
According to the Code of good practice, the goal of a breeding program is (EFFAB, 2010): "Breeding Organizations attempt to produce the most appropriate genetically improved livestock for the purpose in question. Breeding Organizations attempt to select animals that can produce in an economically viable way, and that make efficient use of food and other resources. Breeding Organizations attempt to increase feed efficiency, which reduces the emission of minerals (N, P) into the environment. Breeding Organizations attempt to prevent unintentional matings between domesticated and wild animals of the same species."

Environmental concerns are also of major importance for the future. As emphasized by Kanis et al. (2005), the quantity of minerals and heavy metals excreted in manure per kilogram of meat produced largely depends on production and reproduction efficiencies. In particular, improving growth rate and feed efficiency have a favorable environmental impact (Kanis et al., 2005).

(3) Is the breeding program feasible within 10 years?

In section 8.2 (Phenotypic consequences of selection) we already mentioned that moving from the average to the top 10%, takes about five years of selection and breeding. The top 10% sows, according to the proposed selection index as depicted in Table 8.13, showed no negative consequences of selection for the traits studied. Five years is already halfway the desired vista. The fear that physiological limits on the offspring side are close to be met, as mentioned by Prunier et al. (2010), is not endorsed by this phenotypic tabulation nor by our simulations. Prunier et al. (2010) underpins approaching physiological limits by stating that increased litter size is associated with increased mortality until weaning (stillborn as well as pre-weaning mortality). Based on our simulation (see 8.3), the absolute number of piglets that die until weaning is expected to decrease slightly while litter size still increases. The physiological limits on the mother side, as far as it concerns leg weakness, will be captured by including stayability in the breeding objective. Nutritional deficits because of elevated demands should be accounted for while formulating gestation diets.

(4) Are there reasonable alternatives?

The word 'reasonable' is not free of value judgments. Inside the market, there are no alternatives for genetic improvement of animals other than executing a breeding program. The techniques described in this thesis refer to conventional breeding. Alternative techniques like using DNA information or transgenesis can be used instead or used simultaneously. Transgenesis is a new technology that is currently not used by pig breeding organizations. The use of DNA information will likely speed up genetic improvement. DNA information is used successfully to identify animals that carry genetic defects.

It is clear that for example the Slow Food Organization disagrees on having no reasonable alternative. This organization feels (amongst others) "committed to protecting traditional and sustainable quality foods, defending the biodiversity of cultivated and wild varieties as well as cultivation and processing methods" (Slow food, 2011). One can imagine that 'random mating' is considered a reasonable alternative for genetic improvement to achieve their goals.

(5) Can the breeding program cause harm to the health or welfare of the animal?

The reason for raising the question whether weight loss during lactation should be avoided by adapting the breeding objective is the fear for negative effects on traits not included in the breeding objective. Health or welfare or both might be such traits. Animals with an undisturbed high production will have a higher chance to be selected. Selection for survival until the age animals produce offspring can serve as a kind of natural selection on fitness. Applying the social interaction theory (Chapter 5), animal welfare might even benefit. In other words, animal health and welfare might even benefit from index selection. On the other hand we lack the scientific facts to support these ideas. Intuitively, animal health and welfare are the traits most at risk while allowing sows to loose unbridled weight during lactation. The resource allocation theory might support this idea.

Weight loss during reproduction is commonly observed in all species. Ankney and MacInnes (1978) for example, found average weight losses of 42% in Lesser Snow Geese from arrival on the breeding grounds after spring migration to late incubation. Weight losses of 42% of spring body weight are near the limit a goose can tolerate and it is suggested that such stress may reduce incubation drive and lead to inattentiveness or desertion (so-called failed-nesters). Failed-nesters had utilized all their depot fat and their average body weight was 48% less than that of arriving females. In some cases incubation drive may be strong enough to cause a goose to remain on the nest until she dies of starvation. These birds were in significantly poorer condition than successful females and failed-nesters. Their average weight was 58% less than that of arriving females (Ankney and MacInnes, 1978).

By domestication, humans created a responsibility towards the animals under their custody (duty of care). Duty of care also means the responsibility to protect animals against hardship of nature. Therefore, weight losses of species in their natural environment can not be compared or allowed to captive animals. Nevertheless, the 10% sows that lost most weight in our study lost 'only' 14% of the empty body weight after farrowing during the subsequent lactation (see Appendix; Table A8.2). Although the reproductive cycle of geese is different from pigs, this geese example shows that from a physiological point of view, there seems to be room for weight fluctuations.

(6) Does the breeding program affect the integrity of the animal?
Rutgers and Heeger (1999) defined three criteria to point to respect for animal's integrity: (1) People should not interfere with the wholeness and completeness of animals, (2) should not disrupt the species-specific balance (the ability to lead a normal and natural live), (3) and should not deprive animals of the ability to maintain themselves independently in an environment suitable to the species.

In conventional breeding programs, the selection candidates' own performance and the performance of their relatives are measured for several traits. Breeding values are estimated from these data. A combination of breeding values for several traits can be combined into a selection index, and the animals with the best index are selected for breeding. Breeding organizations attempt to identify animals without errors, to keep accurate records, and to improve data recording. Animal identification and trait recording are fundamental for all breeding programs. Trait recording can be done within a breeding unit or organized as field recording on the (crossbred) end product. Recording and use of phenotypic data is the major driving force for genetic progress. This genetic progress is very much dependent on the accuracy of the data.

The breeding units and farms where field recording is organized should be spread over different management, health status, housing etcetera. Animals from families who perform in a variety of environments will prevail and thus prevent that the population becomes dependent on a specific environment (the selection environment). This does not necessarily mean that breeding for specific circumstances (for example tropical versus moderate climate) should be avoided.

The chance that one of the three criteria as defined by Rutgers and Heeger is violated by applying a conventional breeding program is very small. Only unilateral selection for a large number of generations might impair animal's integrity on the long run.

Unilateral selection for litter size, applying a breeding program as described in Box 8.3, yields a genetic progress of 0.41 piglets per litter per year. Percentage stillborn increases by 0.7% and pre-weaning mortality by 0.4%. Using the Dutch average over 2009 (Table A8.1), increased mortality causes that only 46% of the extra piglets born will survive until weaning. Comparing the average to the top 10% sows when grouping sows on litter size, similar to section 8.2, gives a much clearer picture. Litter size of the top 10% sows is 5.1 piglets higher (18.3 compared to 13.2). Percentage stillborn (10.0% versus 6.3%) and pre-weaning mortality (19.0% versus 10.7%) increased as well. This results in 13.3 piglets weaned per litter for the top 10% sows compared to 11.0 for the average group of sows. Of the 5.1 extra

piglets born, only 2.3 were weaned (45%). One of the reasons for increased mortality is a decreased birth weight. Comparing the average to the top 10% is accompanied by a decreased birth weight of 160 g per piglet. In case of unilateral selection one could argue that physiological limits at the offspring side are close to being met as suggested by Prunier et al. (2010) and thus animal's wholeness and completeness are close to being violated. Whereas a balanced breeding objective prevents negative side effects of genetic selection and, therefore, does not impair the integrity of the animal.

The ability of sows to lead a normal and natural live (the second criterion of the integrity concept of Rutgers and Heeger), is not expected to be affected by an increase in weight loss. Weight loss per se is not uncommon, neither in nature nor in animal husbandry, and thus not a threat for the ability to lead a normal and natural live. At least, as long it does not affect animal's health and welfare. The possible consequences on animal's health and welfare are already discussed while answering Question 5 of the decision support model. Feed intake capacity of sows during gestation is large enough to recover from weight loss during the previous lactation. If weight loss will increase as a consequence of genetic selection, feeding schemes should be adapted though.

As mentioned before, measuring of selection candidate's own performance and the performance of relatives is of the utmost importance for a conventional breeding program. If the variation of environments in which these data are measured is wide enough there is no reason to expect that animals will loose their ability to maintain themselves independently in an environment suitable to the species (the third criterion of the integrity concept).

(7) Is food safety and public health guaranteed?
The Code of Good Practice for Farm Animal Breeding and Reproduction Organizations stated on the item of public health: "The direct possibilities for influencing food safety and public health by farm animal breeding and reproduction are limited. Breeding Organizations are aware of the constant danger of transmitting diseases from one animal generation to another, and attempt to minimize these risks. Breeding Organizations attempt to improve the animals' natural genetic resistance to disease, which reduces the need for medication and the occurrence of zoo noses and improves food safety and human health."

(8) Is biodiversity guaranteed?
On the item of biodiversity the Code of Good Practice stated: "Breeding programs are designed to make optimal use of existing genetic variation between and within

populations. Therefore, Breeding Organizations attempt to maintain genetic diversity in their breeding populations, and to monitor and control the rate of inbreeding. Moreover, Breeding Organizations will contribute semen and/or embryos to (national) gene banks for relevant breeds/lines to ensure conservation of biodiversity" (EFFAB, 2010).

The fact remains that if market share of the large global breeding companies increases, local breeds will be threatened with extinction. This is considered the responsibility of local authorities or private organizations rather than the breeding organization.

Final ethical weighing

The question of negative effects of selection for feed efficiency, leanness and high prolificacy on sow's sensitivity to stress, behavioral disorders and diseases as a possible consequence of increased weight loss during lactation is raised but needed further (scientific) investigation. Scientific prove of undesired side effects of executing a breeding program in general or of increased weight loss in particular is missing.

The future competitiveness of breeding companies depends on continued genetic improvement in the efficiency of quality lean production. To achieve this, no alternatives other than executing a breeding program are available. Adaptations in animal husbandry like feeding and health care might be needed to allow animals to express their genetic potential. Executing a conventional breeding program, applying a balanced breeding objective, is not expected to harm the animals involved in any way, although, weight loss of sows during lactation is expected to increase. Weight loss during reproduction is commonly observed in all species. From a physiological point of view, there seems to be room for weight fluctuations. Weight loss per se is not the problem. Nevertheless, undesired side effects of weight loss can not be completely ruled out. While weighing the interests of the animals, elementary needs of animals such as ensured animal's welfare, recognizing the intrinsic value of animals and the duty of care by humans are included in the assessment and be deemed no risk to the animal by executing a conventional breeding program. Food safety, public health or biodiversity are not jeopardized in any way.

To be able to explain the goals and practices of breeding organizations to the public, breeding organizations should adapt ethics in their business operations. This also implies being transparent about technical and economical aspects of their breeding program towards the society. Tools for breeding companies to fill in this responsibility are:

1. Use the (top) nucleus population to produce a (crossbred) monitoring population, to ensure that the monitor population is at least a generation ahead of the commercial product which is sold today in the market. More than one monitoring population should preferably be available to check under different management or climatologically circumstances depending on the markets a breeding company is selling breeding stock.

2. Detailed recording on animal performance, behavior and health of animals under day to day practical circumstances on the monitoring population should be organized. Data recording should not only be on the traits included in the breeding objective. It should also include traits which are not included but by which one is able to evaluate the consequences of selection. Thus enabling to signalize undesired side effects on the shortest possible notice. This data collection can simultaneously serve to study the underlying physiological processes on which selections acts.

If breeding organizations live up to the aforementioned recommendations, there is only a very small risk on possible damage for the animal by applying an economical breeding objective as depicted in Table 8.11. And if undesired side effects unexpectedly occur, there is the possibility to interfere at an early stage. Weighing the advantages for the breeding organization and the farmers or integrators against the possible negative side effects for the animal, there is no impediment for applying an economical breeding objective, allowing for increased weight losses of sows during lactation.

Acknowledgement

8.5   General conclusions

In section 8.2 it was concluded that weight losses during lactation are "manageable", meaning that high weight losses can be dealt with without impaired fertility results in the next cycle. Results suggest that the driving force behind weight losses is an optimum fat to protein ratio at weaning. This fat to protein ratio depends on the leanness (fatness) of the sow. Genetic selection for lean and efficient grower-finishers will increase leanness of sows. Lean sows compensate their inability to mobilize fat stores by a higher feed intake and higher feed

efficiency. A higher susceptibility (less robustness) of lean sows can not be completely ruled out.

The latter conclusion raises the question whether consequences of selection reach the physiological limits of sows. Section 8.2 demonstrated that there is no reason to expect reaching of this physiological limit to piglet production within the foreseeable future (at least five years in the perspective of the analyses performed). Nevertheless, in extreme situations some risks may become visible. (i) Selection for lactation efficiency will reduce feed intake, and as a consequence protein intake, to such and extend that milk production of sows will be impaired. An increased protein level in the lactation or gestation diets or in both is a short term solution. (ii) Data of sows which show a high feed intake during lactation suggest that piglet production was uncomplicated during and after high feed intake lactation. Sows become less energy efficient though, thus increasing the ecological footprint of pig production. Besides, genetic selection for increased feed intake during lactation will reduce the stayability of sows. This indicates a physiological limit, although this phenomenon is not yet fully understood. (iii) High milk yields of sows facilitate high piglet production. It also reduces pre-weaning mortality of piglets. High birth weight of piglets is by far the most important stimulus for milk production of the sow during early lactation. If we force sows without sufficient milk production capacity to nurse piglets with a high birth weight, this may impair fertility during the next parity. This points to a physiological limit. High milk production in itself does not show any negative side effects. It was concluded that selection for higher birth weight should be accompanied by, at least, selection for increased milk yield. In general, unilateral selection should be avoided and the aim should be for balanced genetic selection to prevent possible negative side effects.

The simulated breeding program in section 8.3 demonstrated that a traditional breeding program yields a balanced genetic progress. All traits included in the breeding objective changed in the desired direction, except feed intake of grower-finishers. Nevertheless, feed:gain ratio improved. The risk of a traditional breeding program also clearly shows for sows. Feed intake during lactation does not keep pace with the increased piglet production with an increased weight loss as a consequence. After ten years of selection, sows weight loss during lactation will increase by 7 kg from about 14 to 21 kg. Feed intake during growing-finishing and during lactation can genetically be altered independently since the genetic correlation is low.

Possible side effects of genetic selection like decreased feed intake during lactation or increased weight loss can relatively easy be accounted for in a breeding program. Genetic correlations between the studied characteristics are such that

dramatic deterioration for each trait can be avoided, while improving other economically important traits. Nevertheless, each deviation from the economically optimum breeding objective goes at the cost of cost price reduction of the slaughter pig. Inclusion of traits to prevent possible side effects of genetic selection in the breeding objective should be considered for other reasons than an economical one, for example an ethical one.

In Section 8.4 it was concluded that by applying the ethical decision support model of the RDA, there is no objection to executing a conventional breeding program allowing for increased weight loss of sows during lactation. The future competitiveness of breeding companies depends on continued genetic improvement in the efficiency of quality lean production. To achieve this, no alternatives other than executing a breeding program are available. Adaptations in animal husbandry like feeding and health care might be needed to allow animals to express their genetic potential. Executing a conventional breeding program, applying a balanced breeding objective, is not to expect to harm the animals involved in any way, although, we can not completely overlook the consequences of ever increasing weight loss. While applying the decision support model, elementary needs of animals such as ensured animal's welfare, recognizing the intrinsic value of animals and the duty of care by humans are included in the assessment and be deemed no risk to the animal. Food safety, public health or biodiversity are not jeopardized in any way. Whatever choices are made, future genetic improvement should be accompanied by a detailed monitoring of possible negative side effects of genetic selection on traits not included in the breeding objective.

In the general introduction it was hypothesized that including feed intake or feed efficiency during lactation or both in the breeding objective for dam lines is necessary to facilitate sow's future increase of unproblematic production of grower-finishers that efficiently convert feed into meat. Also in literature, already in the late 1990's a plea was made (Noblet et al., 1998; Eissen 2000) for genetic selection on higher feed intake of sows during lactation. Results of this thesis show that feed intake of sows during lactation is not an immediate risk for further improvement of more and heavier piglets. Worldwide increase in number of piglets weaned per sow per year since late 1990's (see e.g. general introduction) underlines that feed intake of sows during lactation is not limiting for production increases. Higher piglet production is still on its way via the genetic pipeline and will continue to increase by selection for more and heavier piglets. Selection for increased milk production or litter weight gain is preferred; this will lead to increased protein and energy demands as well. At all events, sows need to eat

more and be more efficient at the same time to keep up with this increased demand. It is a question of tuning the breeding objective in order to optimize the relation between feed intake and body weight losses during lactation.

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Appendix

Table A8.1 Production numbers of the IPG-farm compared to the Dutch average over 2009. Dutch averages after Bedrijfsvergelijking Agrovision B.V. (Kengetallenspiegel, 2010).

	Dutch average	IPG-farm
Number of farms	803	1
Number of sows present	359	165
Number of litters per sow per year	2.37	2.39
Number of piglets weaned per sow per year	27.3	27.5
Age at 1st insemination gilts, d	257	238
Replacement rate sows, %	42	52
Non-return 56 days, %	91	96
Farrowing rate, %	86	94
Interval weaning – 1st insemination, d	5.6	5.3
Interval 1st insemination – pregnancy, d	3.3	0.8
Lactation length, d	25.2	26.2
Parity	4.0	2.7
Percentage primiparous litters, %	18	25
Number of live born piglets per litter	13.2	12.8
Number of stillborn piglets per litter	1.1	0.8
Pre-weaning mortality, %	12.8	8.6
Number of piglets weaned per litter	11.5	11.7
Mortality in nursery, %	1.9	1.0
Piglet weight at sales or start grower phase, kg	25.0	26.4
Age at sales or start grower phase, d	76	71

Table A8.2 Sow performances (Least Squares Means) ordered and grouped according to their weight loss during lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Weight loss is pre-corrected for genetic line, parity of the sow, Herd Year Season and lactation length.

Trait	Classification: Weight loss [1]				
	10% lowest	*20% low*	*40% average*	*20% high*	*10% highest*
Number of lactations	198	397	793	397	199
Weight loss during lactation, kg/25 d	-5.3	6.7	16.1	25.0	33.1
Parity	3.4	3.5	3.4	3.4	3.5
Empty weight sow at farrowing, kg	221^a	225^b	229^c	234^d	237^e
Backfat thickness at farrowing, mm	17.4^a	17.9^b	18.4^c	18.9^d	19.3^d
Fat mass at farrowing, kg	44.3^a	45.5^b	47.0^c	48.4^d	49.3^e
Protein mass at farrowing, kg	34.2^a	34.8^b	35.4^c	36.0^d	36.4^e
Fat to protein ratio at farrowing	1.31^a	1.33^a	1.35^b	1.36^{bc}	1.38^c
Gestation length, d	115.7^a	115.7^a	115.7^a	115.8^a	115.9^a
Total number born	14.2^a	13.9^a	13.4^b	13.2^{bc}	13.0^c
Stillborn, %	6.3^{ab}	6.7^a	6.5^a	6.1^{ab}	4.9^b
Litter weight before cross fostering, kg	18.7^a	18.4^a	18.5^a	18.6^a	18.8^a
Avg. birth weight before cross fostering, kg	1.37^a	1.38^a	1.43^b	1.46^c	1.51^c
STD birth weight before cross fostering, g	296^{ab}	296^{ab}	292^a	296^{ab}	306^b
Number of piglets to be nursed	12.4^a	12.2^{ab}	12.0^{bc}	11.9^c	12.0^{bc}
Litter weight after cross fostering, kg	16.0^a	16.2^a	17.2^b	17.9^c	18.8^d
Avg. birth weight after cross fostering, kg	1.31^a	1.35^a	1.44^b	1.51^c	1.58^d
STD birth weight after cross fostering, g	254^a	231^b	231^b	228^b	235^b
Feed intake during lactation, kg	133^a	132^a	130^b	126^c	119^d
Adjusted weaning weight sow, kg	226^a	219^b	214^c	210^d	204^e
Backfat thickness at weaning, mm	15.3^a	15.1^{ab}	14.9^b	14.8^{bc}	14.6^c
Fat mass at weaning, kg	40.8^a	39.6^b	38.8^c	38.2^d	37.0^e
Protein mass at weaning, kg	35.8^a	34.7^b	33.9^c	33.3^d	32.3^e
Fat to protein ratio at weaning	1.15^a	1.15^a	1.15^a	1.16^a	1.16^a
Fat loss during lactation, kg	3.3^a	5.7^b	8.2^c	10.4^d	12.3^e
Protein loss during lactation, kg	-1.6^a	0.2^b	1.5^c	2.8^d	4.2^e
Input, MJ ME/d	48.4^a	54.2^b	57.9^c	60.6^d	61.2^d
Pre-weaning mortality (%)	19.8^a	14.2^b	10.5^c	8.2^d	7.1^d
Number of piglets weaned	9.7^a	10.3^b	10.6^c	10.9^d	11.1^e
Litter weight gain, kg	54.3^a	60.4^b	64.6^c	67.0^d	68.9^e
STD weaning weight, g	1270^a	1231^a	1217^a	1211^a	1235^a
Milk yield, MJ ME/d	47.5^a	51.7^b	54.9^c	56.3^d	57.8^e
Output, MJ ME/d	37.3^a	40.6^b	43.1^c	44.2^d	45.4^e
Lactation efficiency, %	75^a	75^a	75^a	74^a	75^a
Survival current cycle, %	76^a	81^b	85^c	83^c	83^c
Prolonged interval weaning-estrus, %	8.5^a	8.4^a	10.8^a	8.9^a	7.6^a
Farrowing rate of 1st ins. next parity, %	92^a	90^a	89^a	92^a	89^a
Total number born next parity	13.6^a	13.9^a	13.6^a	13.7^a	13.5^a
Number of piglets per 1st insemination	13.1^a	13.2^a	12.7^a	13.1^a	12.8^a

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

Table A8.3 Sow performances (Least Squares Means) ordered and grouped according to their fatness at start of lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Percentage fat is pre-corrected for genetic line, parity of the sow and Herd Year Season of the litter.

Trait	Classification: % Fat [1]				
	10% leanest	*20% lean*	*40% average*	*20% fat*	*10% fattest*
Number of lactations	203	406	814	406	204
% fat at farrowing	16.3	18.3	20.6	22.9	25.5
Parity	3.5	3.5	3.2	3.4	3.6
Empty weight sow at farrowing, kg	218^a	226^b	229^c	234^d	236^e
Back fat thickness at farrowing, mm	13.1^a	15.7^b	18.2^c	21.1^d	24.1^e
Fat mass at farrowing, kg	35.9^a	41.6^b	46.7^c	52.5^d	58.3^e
Protein mass at farrowing, kg	35.0^{ac}	35.6^b	35.5^b	35.4^{ab}	34.9^c
Fat to protein ratio at farrowing	1.01^a	1.17^b	1.33^c	1.52^d	1.73^e
Gestation length, d	115.7^{ab}	115.6^a	115.8^b	115.7^{ab}	115.8^{ab}
Total number born	13.8^{ab}	13.9^a	13.4^b	13.4^b	13.2^b
Stillborn, %	6.8^a	7.0^a	6.0^{ab}	6.7^a	4.9^b
Litter weight before cross fostering, kg	19.0^{ab}	19.0^a	18.5^{bc}	18.2^c	18.3^{bc}
Avg. birth weight before cross fostering, kg	1.44^a	1.42^a	1.43^a	1.42^a	1.44^a
STD birth weight before cross fostering, g	297^a	301^a	294^a	295^a	290^a
Number of piglets to be nursed	12.2^a	12.2^a	12.0^a	12.1^a	12.0^a
Litter weight after cross fostering, kg	17.5^a	17.2^a	17.1^a	17.2^a	17.1^a
Avg. birth weight after cross fostering, kg	1.43^a	1.42^a	1.44^a	1.44^a	1.44^a
STD birth weight after cross fostering, g	239^a	236^a	229^a	236^a	240^a
Feed intake during lactation, kg	132^a	131^a	129^b	127^{bc}	125^c
Adjusted weaning weight sow, kg	208^a	212^b	215^c	217^d	220^e
Back fat thickness at weaning, mm	11.8^a	13.3^b	14.9^c	16.6^d	18.1^e
Fat mass at weaning, kg	32.4^a	35.7^b	38.8^c	42.1^d	45.3^e
Protein mass at weaning, kg	33.7^a	33.9^a	34.0^a	34.0^a	34.1^a
Fat to protein ratio at weaning	0.95^a	1.05^b	1.15^c	1.27^d	1.37^e
Weight loss during lactation, kg	11.7^a	14.5^b	14.7^b	16.4^b	15.1^{bc}
Fat loss during lactation, kg	4.4^a	6.3^b	7.9^c	10.0^d	12.3^e
Protein loss during lactation, kg	1.5^a	1.7^a	1.5^a	1.5^a	0.9^b
Input, MJ ME/d	53.3^a	55.8^b	56.7^b	59.0^c	60.6^c
Pre-weaning mortality, %	12.4^a	12.1^a	11.3^a	10.6^a	11.7^a
Number of piglets weaned	10.5^a	10.6^a	10.5^a	10.6^a	10.5^a
Litter weight gain, kg	63.4^{ab}	63.6^{ab}	63.7^{ab}	64.3^a	62.2^b
STD weaning weight, g	1183^a	1226^a	1232^a	1232^a	1196^a
Milk yield, MJ ME/d	53.8^{ab}	54.0^{ab}	53.9^{ab}	54.7^a	52.8^b
Output, MJ ME/d	42.4^{ab}	42.4^{ab}	42.3^{ab}	42.8^a	41.6^b
Lactation efficiency, %	78^a	76^a	76^a	74^b	70^c
Survival current cycle, %	80^a	83^a	83^a	82^a	83^a
Prolonged interval weaning-estrus, %	5.2^a	8.5^{ab}	10.5^b	9.8^{ab}	9.7^{ab}
Farrowing rate of 1st ins. next parity, %	86^a	89^a	90^a	89^a	97^b
Total number born next parity	13.6^a	13.9^a	13.7^a	13.5^a	13.6^a
Number of piglets per 1st insemination	12.6^a	12.9^a	13.0^a	12.8^a	13.3^a

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

Table A8.4 Sow performances (Least Squares Means) ordered and grouped according to their feed intake during lactation (respectively 10, 20, 40, 20 and 10 % of the observations). Feed intake is pre-corrected for genetic line, parity of the sow, Herd Year Season and lactation length.

Trait	Classification: Feed intake [1]				
	10% lowest	*20% low*	*40% average*	*20% high*	*10% highest*
Number of lactations	214	429	857	429	215
Feed intake, kg/25 days	108	119	135	148	156
Parity	3.7	3.4	3.6	3.5	3.5
Empty weight sow at farrowing, kg	233^a	232^a	229^b	227^b	227^b
Backfat thickness at farrowing, mm	19.0^a	18.5^a	18.1^b	17.7^c	17.8^{bc}
Fat mass at farrowing, kg	48.6^a	47.5^b	46.3^c	45.4^d	45.6^{cd}
Protein mass at farrowing, kg	35.9^a	35.8^a	35.4^b	35.3^b	35.3^b
Fat to protein ratio at farrowing	1.36^a	1.34^{ab}	1.32^{bc}	1.31^c	1.32^{bc}
Gestation length, d	115.3^a	115.6^b	115.7^c	115.5^{ab}	115.4^{ab}
Total number born	13.4^{ab}	13.2^{ab}	13.0^a	13.5^b	13.6^b
Stillborn, %	6.2^{ab}	6.9^a	5.8^b	6.0^{ab}	6.5^{ab}
Litter weight before cross fostering, kg	18.6^{ab}	18.4^{ab}	18.4^b	18.9^b	18.8^{ab}
Avg. birth weight before cross fostering, kg	1.43^a	1.46^{ab}	1.46^b	1.45^{ab}	1.43^a
STD birth weight before cross fostering, g	287^a	287^a	294^{ab}	294^{ab}	306^b
Number of piglets to be nursed	12.0^{ab}	11.7^a	11.8^a	11.9^{ab}	12.1^b
Litter weight after cross fostering, kg	17.1^a	17.0^a	17.1^a	17.3^a	17.4^a
Avg. birth weight after cross fostering, kg	1.44^a	1.46^a	1.47^a	1.45^a	1.44^a
STD birth weight after cross fostering, g	240^a	238^a	236^a	237^a	244^a
Adjusted weaning weight sow, kg	212^a	216^b	216^b	217^b	218^b
Backfat thickness at weaning, mm	15.1^{ab}	15.1^a	14.9^{ab}	14.8^b	14.8^{ab}
Fat mass at weaning, kg	39.0^a	39.5^a	39.0^a	38.8^a	38.9^a
Protein mass at weaning, kg	33.5^a	34.2^b	34.3^{bc}	34.4^{bc}	34.6^c
Fat to protein ratio at weaning	1.16^a	1.16^a	1.14^a	1.14^a	1.14^a
Weight loss during lactation, kg	21.4^a	15.5^b	12.8^c	10.5^d	10.2^d
Fat loss during lactation, kg	9.7^a	8.1^b	7.4^c	6.5^d	7.0^{cd}
Protein loss during lactation, kg	2.4^a	1.6^b	1.2^c	0.9^d	0.8^d
Input, MJ ME/d	46.3^a	51.9^b	57.9^c	61.2^d	64.9^e
Pre-weaning mortality, %	13.3^a	11.9^a	11.6^a	11.8^a	11.9^a
Number of piglets weaned	10.2^a	10.2^a	10.3^{ab}	10.4^b	10.5^b
Litter weight gain, kg	57.3^a	60.5^b	63.4^c	64.6^d	66.6^e
STD weaning weight, g	1266^a	1266^a	1244^a	1273^a	1279^a
Milk yield, MJ ME/d	49.5^a	51.7^b	53.9^c	54.8^d	56.5^e
Output, MJ ME/d	39.3^a	40.6^b	42.3^c	43.0^d	44.2^e
Lactation efficiency, %	84^a	79^b	74^c	71^d	68^e
Survival current cycle, %	77^a	85^b	85^b	85^b	84^b
Prolonged interval weaning-estrus, %	8.9^{abc}	11.6^a	9.8^{ab}	6.6^{bc}	4.2^c
Farrowing rate of 1st ins. next parity, %	88^a	86^a	87^a	85^a	89^a
Total number born next parity	13.6^{ab}	13.2^a	13.6^{ab}	13.8^b	13.8^b
Number of piglets per 1st insemination	12.9^a	12.1^b	12.3^{ab}	12.5^{ab}	12.8^{ab}

[1] Columns, within a row, with no common letter as suffix, differ significantly (p<0.05).

Table A8.5 Sow performances (Least Squares Means) ordered and grouped according to their estimated milk yield (respectively 10, 20, 40, 20 and 10 % of the observations). Estimated milk yield is pre-corrected for genetic line, parity of the sow, Herd Year Season and lactation length.

Trait	Classification: Estimated milk yield [1]				
	10% lowest	*20% low*	*40% average*	*20% high*	*10% highest*
Number of lactations	268	536	1071	537	268
Milk yield, MJ ME/d	40.3	47.7	54.7	60.2	65.1
Parity	3.5	3.4	3.3	3.3	3.6
Empty weight sow at farrowing, kg	228^a	229^a	229^a	229^a	230^a
Backfat thickness at farrowing, mm	18.1^a	18.2^a	18.5^{ab}	18.6^b	18.6^{ab}
Fat mass at farrowing, kg	46.2^a	46.5^{ab}	47.1^{ab}	47.3^b	47.2^{ab}
Protein mass at farrowing, kg	35.2^a	35.4^a	35.4^a	35.4^a	35.5^a
Fat to protein ratio at farrowing	1.33^a	1.33^a	1.35^{ab}	1.36^b	1.35^{ab}
Gestation length, d	115.4^a	115.6^{ab}	115.6^b	115.7^b	115.7^b
Total number born	13.8^a	13.7^a	13.3^b	13.3^b	13.1^b
Stillborn, %	7.8^a	6.9^a	6.0^b	5.6^b	5.4^b
Litter weight before cross fostering, kg	18.6^{ab}	18.6^{ab}	18.5^a	18.9^{bc}	19.3^c
Avg. birth weight before cross fostering, kg	1.40^a	1.40^a	1.44^b	1.48^c	1.52^d
STD birth weight before cross fostering, g	294^a	293^a	293^a	292^a	294^a
Number of piglets to be nursed	11.9^a	11.9^a	12.0^{ab}	12.1^{bc}	12.3^c
Litter weight after cross fostering, kg	15.2^a	16.1^b	17.2^c	18.4^d	19.6^e
Avg. birth weight after cross fostering, kg	1.30^a	1.37^b	1.45^c	1.53^d	1.60^e
STD birth weight after cross fostering, g	248^a	237^{ab}	237^{ab}	236^{ab}	231^b
Feed intake during lactation, kg	121^a	125^b	128^c	132^d	135^e
Adjusted weaning weight sow, kg	224^a	218^b	214^c	211^d	208^e
Backfat thickness at weaning, mm	15.6^a	15.3^{ab}	15.0^b	14.5^c	14.3^c
Fat mass at weaning, kg	41.1^a	39.9^b	39.0^c	37.7^d	36.9^e
Protein mass at weaning, kg	35.4^a	34.5^b	33.9^c	33.4^d	33.0^e
Fat to protein ration at weaning	1.17^{ab}	1.17^a	1.16^a	1.14^{bc}	1.13^c
Weight loss during lactation, kg	3.9^a	10.3^b	15.2^c	18.7^d	22.1^e
Fat loss during lactation, kg	5.2^a	6.5^b	8.1^c	9.4^d	10.2^e
Protein loss during lactation, kg	-0.1^a	0.9^b	1.5^c	2.0^d	2.5^e
Input, MJ ME/d	46.9^a	51.9^b	57.2^c	61.5^d	65.4^e
Pre-weaning mortality, %	20.8^a	13.9^b	10.6^c	8.1^d	6.0^e
Number of piglets weaned	9.1^a	10.1^b	10.6^c	11.0^d	11.5^e
Litter weight gain, kg	44.6^a	54.8^b	63.8^c	71.4^d	79.0^e
STD weaning weight, g	1329^a	1290^{ab}	1240^c	1246^{bc}	1221^c
Output, MJ ME/d	31.1^a	37.4^b	42.6^c	47.0^d	51.6^e
Lactation efficiency, %	68^a	73^b	75^c	77^d	79^d
Survival current cycle, %	76^a	81^b	84^{bc}	85^c	80^{ab}
Prolonged interval weaning-estrus, %	11.2^a	10.6^a	8.2^a	7.6^a	7.6^a
Farrowing rate of 1st ins. next parity, %	84^a	83^a	84^a	85^a	85^a
Total number born next parity	13.6^a	13.5^a	13.8^a	13.6^a	13.6^a
Number of piglets per 1st insemination	12.6^a	12.5^a	12.7^a	12.4^a	12.7^a

[1] Columns, within a row, with no common letter as suffix, differ significantly ($p<0.05$).

Table A8.6 Sow performances (Least Squares Means) ordered and grouped according to the average birth weight of their piglets after cross fostering (respectively 10, 20, 40, 20 and 10 % of the observations). Average birth weight is pre-corrected for genetic line, Herd Year Season of the litter and parity of the sow.

Trait	Classification: Avg birth wt after cross fostering [1]				
	10% *lowest*	*20%* *low*	*40%* *average*	*20%* *high*	*10%* *highest*
Number of lactations	267	534	1067	535	267
Average birth weight, kg	1.02	1.22	1.45	1.65	1.86
Parity	3.3	3.4	3.4	3.4	3.3
Empty weight sow at farrowing, kg	228^a	228^a	229^a	230^{ab}	232^b
Backfat thickness at farrowing, mm	18.2^a	18.2^a	18.4^a	18.5^a	18.6^a
Fat mass at farrowing, kg	46.4^a	46.6^a	46.9^a	47.3^a	47.5^a
Protein mass at farrowing, kg	35.2^a	35.3^a	35.3^a	35.4^{ab}	35.7^b
Fat to protein ratio at farrowing	1.33^a	1.34^a	1.35^a	1.36^a	1.35^a
Gestation length, d	115.6^{ac}	115.4^b	115.6^a	115.8^c	115.9^d
Total number born	14.5^a	14.8^a	13.7^b	12.4^c	10.6^d
Stillborn, %	6.2^{ab}	7.3^a	6.0^b	5.6^b	6.1^{ab}
Litter weight before cross fostering, kg	18.2^a	18.9^b	18.9^b	18.7^b	17.8^a
Avg. birth weight before cross fostering, kg	1.28^a	1.30^b	1.42^c	1.57^d	1.76^e
STD birth weight before cross fostering, g	309^a	290^b	288^b	295^b	298^{ab}
Number of piglets to be nursed	13.1^a	12.4^b	11.9^c	11.6^d	11.3^e
Litter weight after cross fostering, kg	13.3^a	15.3^b	17.3^c	19.3^d	21.1^e
STD birth weight after cross fostering, g	231^a	246^b	240^{ab}	233^a	232^a
Feed intake during lactation, kg	129^{ac}	126^b	129^c	127^{ab}	129^{ac}
Adjusted weaning weight sow, kg	220^a	217^b	214^c	211^d	210^d
Backfat thickness at weaning, mm	15.4^a	15.1^{ab}	14.9^{bc}	14.7^c	14.6^c
Fat mass at weaning, kg	40.4^a	39.4^b	38.9^b	38.1^c	37.9^c
Protein mass at weaning, kg	34.7^a	34.3^b	33.9^c	33.5^d	33.4^d
Fat to protein ratio at weaning	1.17^a	1.16^{ab}	1.15^{ab}	1.15^b	1.15^{ab}
Weight loss during lactation, kg	7.8^a	11.6^b	14.6^c	18.5^d	21.0^e
Fat loss during lactation, kg	6.0^a	7.1^b	8.1^c	9.3^d	9.5^d
Protein loss during lactation, kg	0.5^a	1.0^b	1.4^c	2.0^d	2.4^e
Input, MJ ME/d	52.8^a	54.4^a	57.2^b	59.5^c	61.2^d
Pre-weaning mortality, %	20.8^a	15.6^b	10.4^c	6.7^d	5.1^d
Number of piglets weaned	10.1^a	10.3^b	10.5^c	10.7^{de}	10.7^{ce}
Litter weight gain, kg	56.5^a	59.7^b	64.1^c	66.7^d	67.9^d
STD weaning weight, g	1270^a	1261^a	1241^a	1273^a	1261^a
Milk yield, MJ ME/d	48.4^a	50.8^b	54.4^c	56.5^d	57.8^e
Output, MJ ME/d	38.2^a	40.0^b	42.7^c	44.4^d	45.5^e
Lactation efficiency, %	73^a	75^a	75^b	76^b	76^b
Survival current cycle, %	85^a	80^b	84^a	83^{ab}	79^b
Prolonged interval weaning-estrus, %	9.6^{ab}	8.2^{ab}	7.2^a	11.5^b	10.3^{ab}
Farrowing rate of 1st ins. next parity, %	85^a	85^a	85^a	82^a	82^a
Total number born next parity	13.6^{abc}	13.9^a	13.6^b	13.6^{ab}	13.1^c
Number of piglets per 1st insemination	12.9^{ab}	13.0^a	12.6^{ab}	12.3^b	11.5^c

[1] Columns, within a row, with no common letter as suffix, differ significantly ($p<0.05$).

Table A8.7 Sow performances (Least Squares Means) ordered and grouped according to their lactation efficiency (respectively 10, 20, 40, 20 and 10 % of the observations). Lactation efficiency is pre-corrected for genetic line, parity of the sow, Herd Year Season and lactation length.

Trait	Classification: Lactation efficiency [1]				
	10% *lowest*	*20%* *low*	*40%* *average*	*20%* *high*	*10%* *highest*
Number of lactations	156	312	625	312	157
Lactation efficiency, %	60	66	71	81	97
Parity	3.7	3.4	3.5	3.7	3.5
Empty weight sow at farrowing, kg	231^{bc}	227^{a}	229^{b}	229^{ab}	233^{c}
Backfat thickness at farrowing, mm	19.2^{a}	18.3^{b}	18.1^{b}	17.7^{c}	17.6^{c}
Fat mass at farrowing, kg	48.6^{a}	46.6^{b}	46.4^{bc}	45.7^{c}	45.9^{bc}
Protein mass at farrowing, kg	35.4^{ab}	35.1^{a}	35.4^{b}	35.6^{b}	36.2^{c}
Fat to protein ratio at farrowing	1.39^{a}	1.34^{b}	1.32^{c}	1.30^{d}	1.28^{d}
Gestation length, d	115.6^{a}	115.7^{a}	115.6^{a}	115.8^{a}	115.7^{a}
Total number born	13.9^{a}	13.2^{bc}	13.4^{ab}	13.0^{c}	13.5^{abc}
Stillborn, %	7.0^{a}	6.4^{ab}	6.5^{a}	5.0^{b}	8.0^{a}
Litter weight before cross fostering, kg	18.7^{ab}	18.3^{ab}	18.6^{a}	18.1^{b}	18.3^{ab}
Avg. birth weight before cross fostering, kg	1.39^{a}	1.44^{bc}	1.44^{bc}	1.45^{c}	1.40^{ab}
STD birth weight before cross fostering, g	309^{a}	301^{ab}	293^{b}	292^{b}	293^{ab}
Number of piglets to be nursed	11.5^{a}	11.8^{ab}	11.9^{b}	12.0^{bc}	12.2^{c}
Litter weight after cross fostering, kg	15.5^{a}	16.8^{b}	17.0^{bc}	17.3^{cd}	17.6^{d}
Avg. birth weight after cross fostering, kg	1.36^{a}	1.43^{b}	1.44^{b}	1.46^{b}	1.44^{b}
STD birth weight after cross fostering, g	242^{a}	232^{ab}	227^{b}	233^{ab}	245^{a}
Feed intake during lactation, kg	134^{a}	134^{a}	131^{b}	125^{c}	117^{d}
Adjusted weaning weight sow, kg	217^{bc}	215^{a}	216^{ab}	216^{ab}	220^{c}
Backfat thickness at weaning, mm	14.3^{a}	14.4^{a}	14.9^{b}	15.1^{b}	15.8^{c}
Fat mass at weaning, kg	38.0^{ab}	37.9^{a}	38.9^{bc}	39.4^{c}	41.1^{d}
Protein mass at weaning, kg	34.6^{b}	34.1^{a}	34.2^{a}	34.2^{a}	34.6^{b}
Fat to protein ratio at weaning	1.10^{a}	1.12^{a}	1.14^{b}	1.16^{c}	1.20^{d}
Weight loss during lactation, kg	14.0^{a}	13.4^{a}	14.1^{a}	13.2^{a}	12.5^{a}
Fat loss during lactation, kg	10.3^{a}	8.8^{b}	7.7^{c}	6.3^{d}	4.6^{e}
Protein loss during lactation, kg	0.9^{a}	1.1^{a}	1.4^{b}	1.4^{b}	1.6^{b}
Input, MJ ME/d	64.2^{a}	61.5^{b}	58.7^{c}	43.3^{d}	46.1^{e}
Pre-weaning mortality, %	13.6^{b}	12.8^{ab}	11.2^{a}	11.7^{ab}	14.0^{b}
Number of piglets weaned	9.8^{a}	10.2^{b}	10.4^{c}	10.4^{c}	10.4^{c}
Litter weight gain, kg	56.8^{a}	60.2^{b}	64.0^{c}	65.0^{c}	63.4^{c}
STD weaning weight, g	1270^{a}	1239^{a}	1210^{a}	1197^{a}	1230^{a}
Milk yield, MJ ME/d	47.5^{a}	51.4^{b}	54.4^{c}	55.3^{d}	54.8^{cd}
Output, MJ ME/d	37.3^{a}	40.4^{b}	42.7^{c}	43.4^{d}	43.0^{cd}
Survival current cycle, %	82^{ab}	87^{a}	84^{a}	85^{a}	79^{b}
Prolonged interval weaning-estrus, %	11.4^{a}	9.6^{a}	7.3^{a}	9.7^{a}	6.6^{a}
Farrowing rate of 1st ins. next parity, %	91^{a}	91^{a}	90^{a}	88^{a}	89^{a}
Total number born next parity	13.4^{a}	13.8^{a}	13.7^{a}	13.5^{a}	13.2^{a}
Number of piglets per 1st insemination	12.6^{a}	12.9^{a}	12.8^{a}	12.4^{a}	12.4^{a}

[1] Columns, within a row, with no common letter as suffix, differ significantly ($p<0.05$).

Summary

Worldwide development makes that breeding companies aim at high productive, self-supporting, robust animals that efficiently convert feed into meat. Current breeding objectives for dam lines might increase the change that the negative energy balance of sows during lactation keeps increasing which on its turn might slow down improvement of piglet production.

It was hypothesized that including feed intake or feed efficiency during lactation or both in the breeding objective for dam lines is necessary to facilitate sow's future increase of unproblematic production of grower-finishers that efficiently convert feed into meat. The aims of this thesis that follow from the hypothesis were therefore:

1. Define feed efficiency of sows during lactation, based on 'on farm' observations;
2. Estimation of genetic parameters for feed efficiency of lactating sows and other lactation performance traits;
3. To investigate the relation between lactation performance and fertility traits and between lactation performance and growing-finishing traits. While analyzing growing finishing traits, recent developments on social interactions will be evaluated.
4. To evaluate the consequences of a traditional breeding program on the expected genetic response on lactation performance;
5. To make a next step towards defining robustness in lactating sows;
6. And finally the general discussion will address the possible physiological limits to genetic selection for lactation traits and evaluates the consequences of alternative breeding objectives.

In Chapter 2 we described the dynamics of body composition of sows and piglets during lactation, and related these traits to a newly introduced trait called "lactation efficiency". Energy metabolism of lactating sows was described, based on on-farm observations of weight and backfat of sows before parturition and at weaning, weight of piglets at birth and at weaning and feed intake of sows during lactation. "Lactation efficiency" was defined as energy efficiency of sows, and calculated for individual sows at two different farms. The average lactation efficiency was 68% and 65% for both farms investigated; meaning that 68 and 65 % of the Metabolisable energy through feed intake or mobilization from body stores, above maintenance of the sow (input), was used for piglet growth and piglet maintenance (output). The association between lactation efficiency and other reproductive traits was studied by estimating the correlations within farms. Sows

with a higher lactation efficiency showed lower feed intake and smaller fat losses. The energy output of efficient sows was slightly higher. The more efficient sows were the better mothers, as mortality of their piglets was lower, piglet growth rate was higher, and at weaning their litters were less variable. Results were remarkably similar for the two farms, despite different feeding strategies. Extra input, by means of feed intake or mobilization from body stores generated extra output by means of litter weight at weaning. This experiment demonstrated that an accurate recording of energy metabolism and relevant reproduction traits with little intervention is possible on commercial farms.

The objective of Chapter 3 was to estimate genetic parameters for lactation efficiency, its underlying traits, and to predict the consequences of current selection strategies in dam lines. The heritability of lactation efficiency was low (0.12). The heritability of lactation feed intake depends on the feeding strategy (0.30 and 0.14 for *ad lib* and restricted feed intake respectively). Body fat mass (0.52) and body weight (0.45) of sows at start of lactation showed the highest heritability. Other traits (sow's body protein mass at start of lactation, litter weight at birth, within-litter SD in birth weight of piglets, sow's weight-, protein- and fat loss and litter weight gain during lactation) showed a low to moderate heritability. Within-litter SD in weaning weight of piglets showed no genetic variability. Selection index theory was used to predict the genetic progress by three alternative breeding programs: (1) A breeding program which aims at balanced progress in total number of piglets born, piglet mortality and % prolonged interval weaning – estrus; (2) Extension of this breeding objective with lactation efficiency; (3) a breeding objective which included only one selection criterion, Litter weight gain, to demonstrate the effect of indirect selection for milk production. It was predicted that a breeding objective for dam lines with emphasis on total number of piglets born, piglet mortality and % prolonged interval weaning – estrus will not dramatically change body weight and body composition at start of lactation, nor mobilization of body tissue and feed intake during lactation. Inclusion of lactation efficiency in the breeding objective will improve stayability as defined by 1st litter survival of sows and lactation efficiency itself without negative consequences for other economically important traits. Nevertheless it might be worthwhile to design a breeding objective where lactation efficiency increases and feed intake remains unchanged.

In Chapter 2 it was hypothesized that the positive phenotypic relation between lactation efficiency and mothering ability of the sow, originates from differences in behavior of sows with a high and low lactation efficiency. The aim of Chapter 4 was to determine the relationship between behaviour of the sow around and after

parturition and the traits litter mortality and feed efficiency during lactation. A total of 78 commercial crossbred sows with parity 1 to 6 and known litter mortality, genetic merit for mothering ability and feed efficiency during lactation were used in this study. Before parturition sows were individually tested in an open field test and an aggression test, where locomotion/position, behaviour and vocalisation were observed during both tests. Around and after parturition, position and behaviour of the sow in the farrowing crate were observed using scan sampling. Phenotypic correlation coefficients were calculated between behaviour during tests and in the farrowing crate, and litter mortality, genetic merit for mothering ability and feed efficiency during lactation. Results showed that position in the farrowing crate was a good indicator for litter mortality, genetic merit for mothering ability and feed efficiency during lactation. Especially one and two weeks after parturition the sows with lower litter mortality and/or higher genetic merit for mothering ability and feed efficiency during lactation were spending more time lying lateral, less sitting and standing, and they had less postural changes. In the aggression test more vocalising and less biting indicated the better sows, whether in the open field test more vocalisation and less lying was observed in the better sows. For the implementation of behavioural observations in selection programs for example to support selection for mothering ability or feed efficiency or both, variance components for behavioural traits have to be estimated and more simple methods to observe large numbers of animals have to be developed.

Social interactions among individuals are ubiquitous both in animals and plants, and in natural as well as domestic populations. These interactions affect both the direction and magnitude of responses to selection, and are a key factor in the design of breeding schemes in agriculture. At present, however, very little is known of the contribution of social effects to heritable variance in trait values. In Chapter 5 we presented estimates of the direct and social genetic variance in daily gain, feed intake, back fat thickness and muscle depth in a population of 14,032 grower-finishers with known pedigree. Results show that social effects contribute the vast majority of heritable variance in daily gain and feed intake in this population. Total heritable variance expressed relative to phenotypic variance equaled 71% for daily gain and 70% for feed intake. These values clearly exceed the usual range of heritability for those traits. Back fat thickness and muscle depth showed no heritable variance due to social effects. Our results suggest that genetic improvement in growing-finishing traits in pigs can be substantially advanced by redirecting breeding schemes, so as to capture heritable variance due to social effects.

The impact of genetic selection for growing-finishing traits on lactation performance traits is still unknown. Therefore, in Chapter 6 genetic correlations between growing-finishing traits and lactation performance traits were estimated. An additional objective was to study the impact of including additive social effects in the animal model on the genetic correlation estimates. The genetic correlation between daily gain of grower-finishers and starting weight of lactating sows was positive (r_g=0.24). The correlation between off test back fat of grower-finishers and fat mass of lactating sows was also positive (r_g=0.53). The genetic regulation of feed intake from the beginning of lactation seems to differ from the genetic regulation of feed intake during the growing-finishing period as the correlation between these two traits was low (r_g=+0.23). It was hypothesized that milk production is an important drive to consume feed. Milk production on its turn is primarily affected by the nursing demand of the suckling piglets during early lactation. With that, control of sow's lactation feed intake is different from feed intake as a grower-finisher. Feed efficiency during growing-finishing and lactation phases showed similar tendencies as the genetic correlation between residual feed intake of the grower-finisher and lactation efficiency of sows was -0.51. Taking heritable social effects into account for daily gain and feed intake did not affect the genetic correlation estimates, neither within growing-finishing traits nor between growing-finishing traits and lactation performance traits. It was concluded that selection for growing-finishing traits in dam lines could be combined with selection for lactation performance traits.

Knowledge on the phenomena that determine feed intake of lactating sows remains important, whether the origin is environmental or genetic. In Chapter 7 we evaluated the effects of climatic parameters on sow's lactation feed intake and evaluated whether the response of sows to variation in temperature on lactation feed intake was heritable. The latter is considered the next step towards defining robustness in lactating sows. A total of 82,614 records for daily feed intake during lactation were available for 848 sows with 3,369 litters. Climatic parameters were available from the nearest weather station, including maximum outside temperature, day length changes and humidity. Although ambient room temperature was modified at the animal level in the farrowing shed, these climatic parameters still had a significant effect on sow's lactation feed intake. Daily feed intake during lactation was described as a function of days in lactation and as a function of both days in lactation and maximum 24 hour outside temperature of the nearest weather station using random regression models. The average heritability and repeatability summarized over the day in lactation at the mean temperature were 0.21 and 0.69 respectively. Genetic variance of temperature

response on feed intake was less than 20% of the day effect. The permanent environmental variance was twofold (day) and fourfold (temperature) higher than the corresponding additive genetic variance. Heritabilities of daily feed intake were higher during the first week of lactation compared to the rest of lactation. The genetic correlation between days decreased as time increased down to about 0.2 between the first and last day in lactation. The genetic correlation between the temperature effects on feed intake remained positive within one standard deviation (+/-) of the temperature. The genetic correlation between feed intake records at the extreme temperatures decreased to about -0.35. It was concluded that random regression models are useful for research and results may be used to develop simpler models that can be implemented in practical breeding programs. An effect of temperature on lactation feed intake was found even in this climate-controlled environment located in a temperate climate zone. Larger effects are expected in more extreme climatic conditions with less temperature-controlled farrowing sheds.

In the general discussion (Chapter 8) the question was raised whether or not physiological limits to piglet production within the foreseeable future (at least five years in the perspective of the analyses performed) are to be expected, provided that unilateral selection is avoided. It was demonstrated that there is no reason to expect reaching these physiological limits. A balanced breeding objective prevents negative side effects of genetic selection, but might increase weight loss and decrease feed intake during lactation. Weight losses during lactation are "manageable", meaning that high weight losses can be dealt with without impaired fertility results in the next cycle. Feed intake of sows during lactation is not limiting for further improvement of more and heavier piglets either. Higher piglet production is still on its way via the genetic pipeline and will continue to increase by selection for more and heavier piglets. Selection for increased milk production or litter weight gain is preferred; this will lead to increased protein and energy demands as well. At all events, sows need to eat more and be more efficient at the same time to keep up with this increased demand. It is a question of tuning the breeding objective in order to optimize the relation between feed intake and body weight losses during lactation.

Samenvatting

Mondiale ontwikkelingen zorgen ervoor dat fokkerijorganisaties zich richten op het fokken van hoogproductieve, zelfredzame, robuuste dieren die efficiënt voer omzetten in vlees. Het huidige fokdoel in zeugenlijnen zou kunnen leiden tot een alsmaar toenemende negatieve energiebalans van zeugen tijdens de zoogperiode. Op zichzelf zou dit de toename in biggenproductie kunnen vertragen.

De hypothese is dat het noodzakelijk is om het kenmerk voeropname of voerefficiëntie tijdens de zoogperiode, of beide, aan het fokdoel voor zeugenlijnen toe te voegen. Hiermee zouden we zeugen in staat stellen de toekomstige toename in productie van vleesbiggen die efficiënt voer omzetten in vlees, probleemloos te kunnen volbrengen.

Vanuit deze hypothese zijn in dit proefschrift de volgende 6 onderzoeksvragen geformuleerd:

1. Kunnen we voerefficiëntie van zogende zeugen, gebaseerd op waarnemingen op praktijkbedrijven, betrouwbaar definiëren?
2. Hoe zien de genetische parameters (erfelijkheidsgraden en genetische correlaties) voor voerefficiëntie van zogende zeugen en andere lactatie gerelateerde kenmerken er uit?
3. Wat is de relatie tussen lactatiekenmerken en vruchtbaarheidseigenschappen en wat is de relatie tussen lactatiekenmerken en vleesvarken kenmerken? Recente ontwikkelingen in andere diersoorten (o.a. legkippen) laten zien dat er kenmerken zijn die beïnvloed worden door genetisch bepaalde sociale interacties tussen hokgenoten. Geldt dit ook voor vleesvarken kenmerken? En zo ja, hoe beïnvloeden die de genetische parameters voor deze eigenschappen?
4. Wat zijn de consequenties van een traditioneel fokprogramma op de verwachte genetische respons op lactatiekenmerken?
5. Zeugen zullen bij hoge temperaturen minder voer opnemen. Is dit genetisch bepaald? Kunnen we deze kennis gebruiken om een vervolgstap te zetten in de richting van het fokken van robuuste zeugen?
6. En ten slotte zal in de algemene discussie de vraag aan de orde komen of er op korte of middellange termijn fysiologische grenzen bereikt worden door genetische selectie. In de algemene discussie zullen ook de consequenties van een aantal alternatieve fokdoelen besproken worden.

In hoofdstuk 2 beschrijven we de dynamiek van de lichaamssamenstelling van zeugen en biggen gedurende de zoogperiode en zullen we deze kenmerken relateren aan een nieuw te definiëren kenmerk "lactatie efficiëntie" genaamd.

Het energie metabolisme van zogende zeugen is beschreven aan de hand van waarnemingen op praktijkbedrijven. Op deze bedrijven zijn lichaamsgewicht en (rug-) spekdikte van zeugen voor het werpen en bij spenen van de biggen geregistreerd. Daarnaast is de voeropname van zeugen tijdens de zoogperiode vastgelegd. Het gewicht van de biggen is verkregen door weging bij de geboorte en bij het spenen van de biggen. "Lactatie efficiëntie" is gedefinieerd als de energie-efficiënte van zeugen, en berekend voor de individuele zeugen op 2 verschillende bedrijven. De gemiddelde lactatie-efficiëntie was 68% en 65% voor beide onderzochte bedrijven. Dit betekent dat 68 respectievelijk 65% van de metaboliseerbare energie uit voeropname of mobilisatie van lichaamsreserves bovenop de onderhoudsbehoefte van de zeug (input) door de zeug gebruikt is om de biggen in hun onderhoud te laten voorzien en te laten groeien (output). De associatie tussen lactatie-efficiëntie en andere vruchtbaarheidseigenschappen is bestudeerd door correlaties te schatten binnen een bedrijf. Zeugen met een hogere lactatie-efficiëntie lieten een lagere voeropname en minder vetverlies zien. De output (vastlegging van energie in biggen) van efficiënte zeugen was licht hoger. De meest efficiënte zeugen waren de betere moeders wat zich uitte in lagere biggensterfte en een hogere biggengroei. Bovendien was de toom biggen uniformer bij spenen. De resultaten van de beide bedrijven vertoonden opvallende gelijkenissen zeker gezien het verschil in voerstrategie van de zeugen tijdens de zoogperiode (onbeperkt versus beperkt). Extra input, door of een hogere voeropname of door meer mobilisatie van lichaamsreserves gaf extra output in de vorm van een hoger toomgewicht bij het spenen van de biggen. Dit experiment demonstreert dat een nauwkeurige registratie van het energiemetabolisme en relevante vruchtbaarheidseigenschappen op praktijkbedrijven met weinig verstoring van de bedrijfsprocessen mogelijk is.

Het doel van hoofdstuk 3 was het schatten van de genetische parameters voor lactatie-efficiëntie inclusief de onderliggende kenmerken en zo de gevolgen te kunnen schatten van de huidige selectie strategieën in zeugenlijnen. De erfelijkheidsgraad van lactatie-efficiëntie was laag (0.12). De erfelijkheidsgraad van voeropname gedurende de zoogperiode is afhankelijk van de voerstrategie (0.30 en 0.14 voor respectievelijk onbeperkte en beperkte voeropname).
Vet massa (0.52) en lichaamsgewicht (0.45) van de zeugen bij de start van de zoogperiode liet de hoogste erfelijkheidsgraad zien. Andere kenmerken (eiwitmassa van de zeug bij de start van de zoogperiode; worpmassa bij geboorte; spreiding in het geboortegewicht binnen de worp; gewicht-, vet-, en eiwitverlies van de zeug tijdens de zoogperiode; gewichtstoename van de toom gedurende de zoogperiode) lieten een lage tot gemiddelde erfelijkheidsgraad zien. De spreiding in

speengewicht van de biggen binnen de toom liet geen genetische variatie zien. Selectie-index theorie is gebruikt om voor drie alternatieve fokprogramma's de genetische vooruitgang te voorspellen. Deze alternatieven waren: (1) Een fokprogramma met een gebalanceerde vooruitgang in het totaal aantal geboren biggen, de biggensterfte en het percentage verlengd interval spenen-dekken; (2) Uitbreiding van dit fokdoel met lactatie-efficiëntie, (3) een fokdoel dat slechts één selectiecriterium omvat, namelijk toomgroei om het effect te demonstreren van indirecte selectie voor melkproductie. Resultaten van de simulatie laten zien dat een fokdoel voor zeugenlijnen met nadruk op het totaal aantal geboren biggen, toomuitval en het interval spenen-dekken, het lichaamsgewicht en de lichaams-samenstelling van zeugen bij de start van de zoogperiode niet wezenlijk zal veranderen, ook mobilisatie van lichaamsreserves en voeropname gedurende de zoogperiode zal niet of nauwelijks veranderen. Het toevoegen van lactatie-efficiëntie aan het fokdoel zal de levensduur van zeugen verbeteren en uiteraard lactatie-efficiëntie zelf, zonder nadelige consequenties voor andere economisch belangrijke kenmerken. Niettemin is het verstandig om een fokdoel te kiezen waarbij de lactatie-efficiëntie verhoogd wordt en de voeropname minimaal niet verslechterd.

In hoofdstuk 2 is de hypothese geformuleerd dat de positieve fenotypische correlatie tussen lactatie-efficiëntie en moedereigenschappen van de zeug zijn oorsprong vindt in verschillen in gedrag tussen zeugen met een hoge of lage lactatie-efficiëntie. Het doel van hoofdstuk 4 is om de relatie tussen het gedrag van de zeug rondom en na de partus en de kenmerken toomuitval gedurende de zoogperiode en lactatie-efficiëntie te beschrijven. In deze studie zijn de gegevens van in totaal 78 commerciële hybride zeugen met een worpnummer tussen 1 en 6, met bekende toomuitval, fokwaarde voor moedereigenschappen en lactatie-efficiëntie gebruikt. Voor de partus zijn de zeugen individueel getest in een open veldtest ('open field-test') en een agressietest. In beide testen zijn de bewegingen, houding als ook het gedrag van de zeug en alle vocale uitingen geobserveerd.
In de kraamstal zijn rondom en na de partus ook houding en gedrag van de zeug geobserveerd door gebruikmaking van 'scan sampling'. Fenotypische correlatie zijn berekend tussen gedrag gedurende de tests en in de kraamstal, biggensterfte, fokwaarde voor moedereigenschappen en lactatie-efficiëntie. Resultaten laten zien dat de houding van de zeug in de kraamstal een goede indicator is voor toomuitval, de fokwaarde voor moedereigenschappen en de lactatie-efficiëntie. Zeugen met een lage toomuitval en/of een hoge fokwaarde voor moedereigenschappen en/of een hoge lactatie-efficiëntie, brachten, een en twee weken na de partus, meer tijd

door met lateraal liggen en minder tijd met zitten en staan en vertoonde minder activiteit in de vorm van verandering van lichaamshouding . In de agressietest waren de betere zeugen diegene die het meeste geluid maakte en minder beten ofschoon in de open veldtest de beste zeugen diegene waren die meer geluid produceerde en minder lagen. Voor de implementatie van gedragsobservaties in selectie programma's (bv. het ondersteunen van selectie op moedereigenschappen of lactatie-efficiëntie of beide) moeten variantiecomponenten voor gedrags-kenmerken geschat worden en simpelere methoden voor observatie van grote aantallen dieren ontwikkeld worden.

Sociale interacties tussen individuen zijn alom tegenwoordig bij zowel dieren als planten, zowel in natuurlijke als gedomesticeerde populaties. Deze interacties beïnvloeden zowel de richting als de omvang van de selectierespons en is de sleutelfactor in het ontwerp van fokprogramma's in de landbouw. Op dit moment echter is erg weinig bekend over de bijdrage van sociale effecten op de genetische variatie in kenmerken.

In hoofdstuk 5 presenteren we schattingen van de directe en sociale genetische variantie in testgroei, voeropname, rugspekdikte en spierdikte in een populatie van 14.032 vleesvarkens met bekende afstamming. Resultaten laten zien dat sociale effecten voor een groot deel bijdragen aan de genetische variantie voor testgroei en voeropname binnen de populatie. De totale erfelijke variantie als percentage van de fenotypische variantie komt uit op ongeveer 71% voor testgroei en 70% voor voeropname. Deze waarden zijn duidelijk hoger dan de gebruikelijke erfelijkheidsgraad voor deze kenmerken. Spek- en spierdikte laten geen genetische variantie zien als gevolg van sociale effecten. Onze resultaten suggereren dat genetische verbetering in vleesvarken eigenschappen substantieel kan versnellen door het aanpassen van fokprogramma's zodat genetische variantie als gevolg van sociale effecten gebruikt wordt.

De impact van genetische selectie voor vleesvarken kenmerken op lactatie kenmerken is nog onbelicht. Daarom zijn in hoofdstuk 6 genetische correlaties geschat tussen vleesvarken kenmerken en lactatiekenmerken. Een bijkomende doelstelling was het bestuderen van de impact van sociale effecten in het diermodel op de schattingen van de genetische correlaties. De genetische correlatie tussen testgroei als vleesvarkens en het gewicht van zeugen bij aanvang van de zoogperiode was positief (r_g=0.24). De correlatie tussen spekdikte van vleesvarkens en de vet massa van zeugen bij aanvang van de zoogperiode was ook positief (r_g=0.53). De genetische regulatie van voeropname vanaf het begin van de

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zoogperiode lijkt verschillend te zijn van de genetische regulatie van voeropname gedurende de mestperiode omdat de correlatie tussen deze twee kenmerken relatief laag was (r_g=+0.23). Het is aannemelijk dat melkproductie een belangrijke drijfveer is voor zeugen om voer op te nemen. Melkproductie op haar beurt wordt primair beïnvloed door de stimulans die uitgaat van zogende biggen gedurende de start van de zoogperiode. Hiermee is het voor de handliggend dat de regulatie van de voeropname van zogende zeugen anders is dan de regulatie van de voeropname van vleesvarkens. Voerefficiëntie gedurende de mest- en zoogperiode lijken in hoge mate hetzelfde kenmerk. De genetische correlatie tussen residuele voeropname van de vleesvarkens en lactatie-efficiëntie van zeugen is hoog (r_g=-0,51). Indien erfelijke sociale effecten onderdeel uitmaken van het genetische model voor testgroei en voeropname, heeft dat geen invloed op de geschatte genetische correlaties, noch binnen vleesvarken kenmerken noch tussen vleesvarken-kenmerken en lactatiekenmerken. De conclusie uit dit onderzoek was dat selectie op vleesvarken kenmerken gecombineerd kan worden met selectie op lactatiekenmerken.

Kennis van de factoren die de voeropname van zeugen tijdens de zoogperiode bepalen blijft onverminderd belangrijk. Het maakt daarbij niet uit of dit omgevingsfactoren zijn of dat het genetische factoren betreft.

In hoofdstuk 7 bestuderen we de invloed van klimatologische omstandigheden op de voeropname van zogende zeugen en bestuderen of de manier waarop zeugen reageren in hun voeropname op temperatuur verschillen erfelijk is. Dat laatste wordt beschouwd als een volgende stap in de definitie van robuustheid bij zogende zeugen. Voor dit onderzoek zijn dagelijkse voeropnames gedurende de zoogperiode beschikbaar van 848 zeugen met 3.369 cycli. Totaal waren er 82.614 dag opnames beschikbaar voor analyse. Weergegevens waren beschikbaar van het dichtstbijzijnde weerstation, met inbegrip van de maximum buitentemperatuur, veranderingen in daglengte en relatieve luchtvochtigheid. Klimaatregeling op dierniveau vond plaats door middel van verwarming en ventilatie per afdeling. Desondanks hadden de weergegevens van het dichtstbijzijnde weerstation nog een significant effect op de voeropname van zogende zeugen. De dagelijkse voeropname gedurende de zoogperiode is beschreven als functie van de dag in lactatie en als functie van zowel de dag alsook de maximale buitentemperatuur van het dichtstbijzijnde weerstation op de dag van de voeropname. Hierbij zijn random regressie modellen gebruikt. De erfelijkheid en herhaalbaarheid, gemiddeld over alle dagen van de zoogperiode bij de gemiddelde temperatuur bedroeg respectievelijk 0.21 en 0.69. De genetische variantie van het temperatuureffect op

voeropname was minder dan 20% van het dag effect. De permanente omgeving variantie was twee keer (dag) en vier keer (temperatuur) zo groot als de corresponderende diervariantie. De erfelijkheidsgraad voor het dag effect op voeropname was hoger gedurende de eerste week van zoogperiode vergeleken met de rest van de zoogperiode. De genetische correlatie tussen voeropnames op de verschillende dagen van de zoogperiode neemt af naarmate de afstand tussen de dagen groter wordt. De genetische correlatie tussen voeropname op de eerste en laatste dag van de zoogperiode is ongeveer 0,20. De genetische correlatie tussen de effecten van temperatuur op voeropname bleef positief binnen een standaard afwijking (+/-) van de temperatuur. De genetische correlatie tussen voeropname bij extreme temperaturen daalde tot ongeveer -0,35. Geconcludeerd kon worden dat random regressie modellen nuttig zijn bij onderzoek en dat de resultaten gebruikt kunnen worden om simpelere modellen te ontwikkelen die geïmplementeerd kunnen worden in praktische fokprogramma's. Zelfs in deze klimaat gecontroleerde stallen in een omgeving met een gematigd klimaat is een (genetisch) effect vastgesteld van temperatuur op de voeropname van zeugen tijdens de zoogperiode. Grotere effecten mogen verwacht worden onder extremere klimatologische omstandigheden met minder temperatuur gecontroleerde kraamstallen.

In de algemene discussie (hoofdstuk 8) is de vraag opgeworpen of wellicht in de nabije toekomst fysieke grenzen te verwachten zijn aan biggenproductie (op termijn van tenminste 5 jaar met het oog op de uitgevoerde analyses) op voorwaarde dat eenzijdige selectie wordt vermeden. Het is aangetoond dat er geen reden is om fysieke grenzen in de nabije toekomst te verwachten. Een gebalanceerd fokdoel voorkomt dat genetische selectie leidt tot ongewenste neveneffecten, maar leidt wellicht tot een toename van het gewichtsverlies en tot een verminderde voeropname gedurende de zoogperiode. Gewichtsverlies gedurende de zoogperiode hoeft geen negatieve consequenties te hebben. Dit betekent dat hoge gewichtsverliezen op kunnen treden zonder verminderde vruchtbaarheidsresultaten in de volgende cyclus. Voeropname van zeugen gedurende de zoogperiode is niet beperkend voor de verdere verbetering van het aantal en het (geboorte-)gewicht van de biggen. De genetische vooruitgang in biggenproductie, zowel qua aantal als ook qua gewicht, gerealiseerd op de nucleus bedrijven zal ook de komende jaren de praktijkbedrijven nog bereiken. Om de toenemende biggenproductie in goede banen te leiden is selectie op verhoogde melkproductie of toomgroei gewenst. Dit zal tevens leiden tot de vraag naar verhoogde eiwit- en energiegehaltes in het zeugenvoer. Hoe dan ook, zeugen

zullen meer moeten eten en zullen tegelijkertijd efficiënter met hun voer moeten omgaan om de verhoogde vraag aan te kunnen. Het is een kwestie van nauwkeurig afstemmen van de fokdoelen om een optimale balans tussen voeropname en verlies van lichaamsgewicht van zeugen tijdens de zoogperiode te bereiken.

P

Publications

Training and Supervision Plan

Curriculum vitae

Dankwoord

Publications

Peer-reviewed publications (last 6 years)

Bergsma, R., E. Kanis, M.W.A. Verstegen, C.M.C. van der Peet – Schwering, and E.F. Knol. 2009. Lactation efficiency as a result of body composition dynamics and feed intake in sows. Livest. Sci.. 125:208-222.

Bergsma, **R**., E. Kanis, E.F. Knol, and P. Bijma. 2008. The contribution of social effects to heritable variation in finishing traits of domestic pigs (*Sus scrofa*). Genetics 178: 1559–1570.

Bergsma, R., E. Kanis, M.W.A. Verstegen, and E.F. Knol. 2008. Genetic parameters and predicted selection results for maternal traits related to lactation efficiency in sows. J. Anim. Sci. 86:1067–1080.

Rens, B.T.T.M. van, G. de Koning, **R. Bergsma**, and T. van der Lende. 2005. Preweaning piglet mortality in relation to placental efficiency. J. Anim. Sci. 83:144-151.

Bouwman, A.C., **R. Bergsma**, N. Duijvesteijn, and P. Bijma. 2010. Maternal and social genetic effects on average daily gain of piglets from birth until weaning. J. Anim Sci. 88:2883-2892.

Abstracts in conference proceedings (last 6 years)

Bergsma, **R**., E. Kanis, M. Verstegen, and E. Knol. 2010. Genetic correlations between lactation performance and growing-finishing traits in pigs. *Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany.* Paper No. 679

Bergsma, **R**., E.F. Knol, N. Duijvesteijn, and P. Bijma. 2008. Application of social effects in a pig breeding program. Kennedy conference, Guelph, Canada.

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Bergsma, R., and E.F. Knol. 2006. Expected genetic gain using lactation efficiency and its components in a breeding program in dam lines. *In:* Book of abstracts of the 57th Annual Meeting of the European association for Animal Production, Antalya, Turkey.

Bergsma, R., and H. Feitsma. 2005. Morphology examination of semen. Proceedings of European A.I. Vets 17th meeting in Cracow, Poland, 12th-15th October 2005, (Conference paper).

Young, J., **R. Bergsma**, E. Knol, J. Patience, and J. Dekkers. 2010. Effect of selection for residual feed intake on sow reproductive performance and lactation efficiency. *Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany.* Paper No. 223.

Camerlink, I., **R. Bergsma**, N. Duijvesteijn, J.E. Bolhuis, and P. Bijma. 2010. Consequences of selection for social genetic effects on ADG in finishing pigs- a pilot study. *Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany.* Paper No. 595.

Canario, L., **R. Bergsma**, R.B. D'Eath, A.B. Lawrence, R. Roehe, N. Lundeheim, L. Rydhmer, E. Knol, and SP Turner. 2009. Genetic associations of group effects for growth, estimated using a cooperation model, with post-mixing agonistic behaviours, skin lesions and activity in pigs. UFAW International Symposium Darwinian selection, selective breeding and the welfare of animals, Bristol, United Kingdom (Accepted).

Rodenburg, T.B., P Bijma, ED Ellen, **R. Bergsma**, S de Vries, JE Bolhuis, B Kemp, and JAM van Arendonk. 2009. Breeding Amiable Animals? Improving Farm Animal Welfare By Including Social Effects Into The Genetic Model. UFAW International Symposium Darwinian selection, selective breeding and the welfare of animals, Bristol, United Kingdom (Accepted).

Bouwman, A.C., **R. Bergsma**, N. Duijvesteijn, and P. Bijma. 2009. The contribution of social effects to heritable variation in average daily gain of piglets from birth till weaning. . *In:* Book of abstracts of the 60th Annual Meeting of the European association for Animal Production, Barcelona, Spain, (Accepted).

Canario, L., **R. Bergsma**, R.B. D'Eath, A.B. Lawrence, R. Roehe, N. Lundeheim, L. Rydhmer, E. Knol, and S.P. Turner. 2008. Genetic relations between the group effect for average daily gain, and post-mixing aggression and skin lesions in Swedish pig. Book of abstracts of the 4th International Workshop on the Assessment of Animal Welfare at Farm and Group Level (WAFL), 10-13 September 2008, Ghent, Belgium pp 42.

Knol, E.F., N. Duijvesteijn, **R. Bergsma**, and P. Bijma. 2008. Application of social effects in a pig breeding program. *In:* Book of abstracts of the 59th Annual Meeting of the European association for Animal Production, Vilnius, Lithuania pp. 201.

Canario, L., R. **Bergsma**, R.B. D'Eath, A.B. Lawrence, R. Roehe, N. Lundeheim, L. Rydhmer, E. Knol, and S.P. Turner. 2008. Genetic relations between the group

effect for average daily gain, and post-mixing aggression and skin lesions in Swedish pigs. *In:* Book of abstracts of the 59th Annual Meeting of the European association for Animal Production, Vilnius, Lithuania pp. 200.

Ellen, E.D., **R. Bergsma**, and P. Bijma. 2008. The contribution of social integrations to heritable variance in laying hens and domestic pigs. *In:* Book of Abstracts of the 20th International Congress of Genetics, Berlin Germany, pp 13.

Engelsma, K.A., **R. Bergsma**, and E.F. Knol. 2007. Genetic parameters for components of boar taint and female fertility. *In:* Book of abstracts of the 58th Annual Meeting of the European association for Animal Production, Dublin, Ireland, pp. 64.

Feitsma, H., **R. Bergsma,** and D.W. Ducro-Steverink. 2006 The effect of morphological abnormal cells on sow fertility, Proceedings of the 19th IPVS congress Copenhagen, Denmark, Abstract No. P. 35-11.

Knol, E.F., D.T. Prins, and **R. Bergsma**. 2005. Relations between lactation-, and slaughter/carcass traits in pigs.. Joint ASAS ADSA CSAS Meeting Cincinnati, Ohio, Abstract no 524.

Feitsma, H., **R. Bergsma,** and A. v.d. Laar. 2005. Effect of morphological abnormal sperm cells on farrowing rate and litter size in pigs. Proceedings of the International conference on pig reproduction, Rolduc Kerkrade, The Netherlands.

Training and supervision plan

Basic package

WIAS Introduction course	exemption
Course on philosophy of science and ethics	exemption

Scientific exposure

International conferences

Annual joint meeting of ASAS, ADSA, PSA St Louis Missouri, USA	2004
Annual meeting of the AIVets Cracow, Poland	2005
Annual meeting of the EAAP Antalya, Turkey	2006
Annual meeting of the EAAP Dublin, Ireland	2007
Kennedy conference Guelph, Canada	2008
World Congress on Genetics (WCGALP), Leipzig Germany	2010

Presentations

Annual joint meeting of ASAS, ADSA, PSA St Louis Missouri, USA (oral)	2004
Annual meeting of the AIVets Cracow, Poland (oral)	2005
Annual meeting of the EAAP Antalya, Turkey (oral)	2006
Annual meeting of the EAAP Dublin, Ireland (oral)	2007
Kennedy conference Guelph, Canada (oral)	2008
F&G connection Vught, The Netherlands (oral)	2008
World Congress. on Genetics (WCGALP), Leipzig Germany (oral)	2010

In-depth studies

Incorporating Competitive Effects, by Bill Muir	2004
QTL Mapping, MAS, and Genomic Selection, by Ben Hayes	2008
Quantitative Genetics discussion group (weekly meetings)	2006-2010

Professional skills support courses

TOPIGS in-company training 'presenteren kun je leren'	2007
Scientific Writing (language Services WUR)	2008

Research skills training

Preparing own PhD research proposal	2005
External training period Armidale, Australia	2008

Didactic skills training

Supervising 4 MSc theses	2006-2008
Supervising 2 EM ABG theses	2008-2009

Total credits: 40

Curriculum vitae

Rob Bergsma is geboren op 8 April 1960 in Sint Laurens (thans gemeente Middelburg), in de provincie Zeeland. Na het voltooien van de Hogere Landbouwschool in Dordrecht en de Hogere kadercursus pluimvee- en varkenshouderij in Almelo, trad hij in dienst als fokkerij-assistent bij het toenmalige Varkens Onderzoek Centrum Nieuw Dalland BV. in Merselo, in de provincie Limburg.

In 1993 trad hij in het huwelijk met Ingrid Heijs. Uit dit huwelijk werden in 1994 Zeb en in 1996 Kiki geboren.

Inmiddels is hij na een aantal fusies in de varkensfokkerijwereld, werkzaam als senior researcher bij het IPG, het Institute for Pig Genetics BV. in Beuningen.

Dankwoord

Met een Hogere Beroeps Opleiding als basis is het starten van een promotieonderzoek niet de meest voor de hand liggende keuze. Bart Molenaar, Hoofd Research, Productontwikkeling en Kwaliteitsbewaking van het toenmalige V.O.C. Nieuw-Dalland, is degene geweest die me destijds op het spoor van een promotieonderzoek gezet heeft. Tijdens de fusiegolf in de varkensfokkerij is het idee op een laag pitje komen te staan. Begin 2000 is het toch weer nieuw leven ingeblazen, in het bijzonder door toedoen van Egbert Knol. Egbert zijn gedachte was daarbij dat het werk toch moest gebeuren. Als ik dan wat extra aandacht zou besteden aan het opschrijven kon ik het wel samenvoegen tot een 'boekje' en voilà. Zo geformuleerd klinkt het simpel. Uiteindelijk heeft het toch meer dan 5 jaar geduurd, al ligt er nergens een formele startdatum vast. 'Ergens' in 2005 ben ik begonnen met mijn onderzoek. Zelf beschouw ik 1 april 2006 als de formele startdatum. Vanaf dat moment had ik 2 dagen per week een bureau bij de vakgroep Fokkerij en Genetica van de Wageningen Universiteit en kwam er structuur in mijn werkzaamheden. Ik heb me daar achteraf vaak over verbaasd maar ik heb me vanaf de eerste dag, niet alleen thuis gevoeld maar voelde me ook een onderdeel van de vakgroep. Ik denk dat dat in belangrijke mate de verdienste is van Johan van Arendonk. Met Egbert Knol en Johan van Arendonk heb ik al 2 mensen van mijn begeleidingscommissie genoemd. Martin Verstegen en Egbert Kanis completeren het viertal. Ik had me geen betere begeleidingscommissie kunnen wensen. Vier mensen met ieder voor zich hun geheel eigen inbreng waarvan ik veel geleerd heb. De bijeenkomsten leverde iedere keer boeiende discussies op en gaf energie. Johan, Martin, Egbert en Egbert bedankt!

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Colophon