

Genetics of Sow Performance in Piglet Production

Helena Lundgren

*Faculty of Veterinary Medicine and Animal Science
Department of Animal Breeding and Genetics
Uppsala*

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2011

Acta Universitatis agriculturae Sueciae

2011:91

Cover illustration by Cano Merkan

ISSN 1652-6880

ISBN 978-91-576-7635-1

© 2011 Helena Lundgren, Uppsala

Print: SLU Service/Repro, Uppsala 2011

Genetics of Sow Performance in Piglet Production

Abstract

The aim of this thesis was to provide knowledge about the genetic relationships concerning sow performance in piglet production. During the last decades, selection in dam lines has focused on increasing litter size and piglet growth.

Consequently, the demand on the sow to provide her piglets with enough milk increases. At the same time, breeding for animals with less fat limits the sow's possibility to store body reserves to be used during lactation. Poor body condition is related to reproduction problems and welfare problems such as shoulder ulcers. In this thesis, piglet growth, feed intake, sow body condition, shoulder ulcers and a number of reproduction traits were studied. Breeding for increased mean piglet weight, as a trait of the sow, will increase weight heterogeneity in the litter. Sows with a genetic ability for high feed intake raise heavy litters. A heavy litter is genetically related to poor body condition of the sow at weaning. Shoulder ulcers in lactating sows is a heritable trait. Sows producing heavier piglets and sows with poor body condition have an increased risk of developing shoulder ulcers. It is important to take into account shoulder ulcers in breeding programs to improve both sow welfare and profitability. Selection for high piglet growth may deteriorate the sow's condition at weaning, which will affect the following reproduction cycle in a negative way. Selection for litter growth or piglet growth (as maternal traits) in 1st litter may prolong the interval from weaning to mating and decrease litter size in 2nd litter.

Maintaining a good body condition is central for sow performance in piglet production and sow body condition should be included in the genetic evaluation to ensure sufficient reproduction and welfare of the sows. Even if selection for improved sow performance in piglet production is important, further development of management and feeding routines is necessary to provide the environment needed for the sows to be able to express their genetic potential.

Keywords: pig, reproduction, genetic correlation, piglet weight, maternal effect, feed intake, body condition, shoulder ulcers, pregnancy

Author's address: Helena Lundgren, SLU,
Department of Animal Breeding and Genetics, P.O. Box 7023, SE-705 07 Uppsala,
Sweden

E-mail: Helena.Lundgren@slu.se

Till Mamma

The aim is to focus...

H. Lundgren

Contents

List of Publications	7
Abbreviations	8
1 Introduction	9
2 General background	11
2.1 Resource allocation and genetic correlations	11
2.2 Piglet growth	12
2.2.1 Litter heterogeneity and piglet growth	12
2.2.2 Milk production	12
2.3 Feed intake, body condition and shoulder ulcers	13
2.3.1 Shoulder ulcers	13
2.4 Production and reproduction	15
3 Aims of the thesis	17
4 Summary of studies	19
4.1 Material and methods	19
4.1.1 Material	19
4.1.2 Traits	20
4.1.3 Methods	22
4.2 Main findings	23
4.2.1 Heritability estimates	23
4.2.2 Genetic correlations	24
5 General discussion	27
5.1 Piglet growth (Paper I)	27
5.1.1 Weight heterogeneity	27
5.1.2 Direct and maternal effects on piglet growth (Paper I and II)	28
5.2 Relationships between feed intake and body condition (Paper IV)	29
5.3 Shoulder ulcers (Paper III)	30
5.4 Production and reproduction	32
5.4.1 Weaning-to-service interval (Paper II and IV)	32
5.4.2 Litter size (paper II and IV)	33
5.5 Recommendations for breeding	34

6	Conclusions	39
7	Future research	41
8	Svensk sammanfattning	43
8.1	Bakgrund	43
8.2	Sammanfattning av studierna	43
	References	47
9	Acknowledgements	53

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Canario, L., Lundgren, H., Haandlykken, M. and Rydhmer, L. (2010). Genetics of growth in piglets and the association with homogeneity of body weight within litters. *Journal of Animal Science* 88, 1240-1247.
- II Lundgren, H., Canario, L., Grandinson, K., Lundeheim, N., Zumbach, B., Vangen O. and Rydhmer, L. (2010). Genetic analysis of reproductive performance in Landrace sows and its correlation to piglet growth. *Livestock Science* 128, 173-178.
- III Lundgren, H., Zumbach, B., Lundeheim, N., Grandinson, K., Vangen, O., Olsen, D. and Rydhmer, L. (2011). Heritability of shoulder ulcers and genetic correlations with mean piglet weight and sow body condition. *Animal*, accepted, doi:10.1017/S1751731111001170, 8 pp.
- IV Lundgren, H., Fikse, W.F., Grandinson, K., Lundeheim, N., Canario, L., Vangen, O., Olsen, D. and Rydhmer, L. Genetic parameters for feed intake, litter weight, body condition and reproduction in Norwegian Landrace sows. (In manuscript)

Papers I-III are reproduced with the permission of the publishers.

Abbreviations

APP	Perception of sow appetite during 3 weeks from start of lactation
BC	Sow body condition score at weaning
BW3	Individual body weight at 3 weeks
DELAYED	Inseminated within one week after weaning
FEED	Sow feed intake at one day in the 3 rd week of lactation
IWG03	Individual piglet weight gain at 3 weeks
IWO	Interval from weaning to oestrus
LW	Litter weight at 3 weeks
MBW3/ meanW3	Mean piglet weight at 3 weeks
MBWB	Mean body weight at birth
NBA	Number of piglets born alive
NBTnext/NBT2	Number of piglets born in second parity
PREGNANT	Pregnant on the first insemination after weaning
PSD	Posterior standard deviation
SD	Standard deviation
SDBW3	Standard deviation in body weight at 3 weeks
SDBWB	Standard deviation in body weight at birth
SE	Standard error
SLS	Second litter syndrome
WSI	Weaning-to-service interval
WSI50	Weaning-to-service interval, 1 – 50 days
WSI7	Weaning-to-service interval, 1 – 7 days

1 Introduction

The pig is amazing! It is both favored and feared due to its ability to reproduce, in almost any environment. In addition, the pig is fast growing and has a high feed efficiency. These features are what make the pig contributing to 40% of the world's meat production (FAO, 2009). The global pig production is increasing for several reasons where the most obvious one is the increased demand for food from an increasing human population (FAO, 2009). Another reason is the fact that the pig is an omnivore and can utilize a broad range of feed, from high quality products supplied in an intense high-tech production system to almost whatever it comes across as a free ranged foraging scavenger. Not only the possibility of using a variety of food sources in a world where resources are limited but also the lower impact on the environment, compared to cattle (Steinfeld et al., 2006), is in favor for pig production. According to FAO (2009), China is by far the largest producer of pig meat and is responsible for more than half (51.9%) of the total yearly pig meat production (115 454 000 tonnes). In Europe, Germany (4.0%) and Spain (2.7%) takes the lead followed by Poland (1.8%) and France (1.7%). In the Nordic countries, Denmark (1.5%) is the largest producer followed by Sweden (0.2%) and Finland (0.2%). Norway produces about 0.1% of the global pig meat production.

In pig breeding, the traits in the breeding goal differs between sire and dam lines. In sire lines emphasis is on production which includes traits like growth, carcass composition and meat quality. Growth and carcass composition are also important for dam lines, together with reproduction traits. There are unfavorable genetic relationships between production and reproduction traits. During the last decades, selection in dam lines has been focused on increasing litter size and piglet growth. Consequently, the demand on the sow to provide her piglets with enough milk increases. At the same time, breeding for animals

with less fat limits the sow's possibility to store body reserves to be used during the energy demanding lactation. Poor body condition is related to reproduction problems (Whittemore, 1996; Prunier et al., 2003) as well as welfare problems (Broom, 1988; Herskin et al., 2010).

The possibility of breeding for increased piglet weights without negative effects on the performance of the sow needs to be explored. The overall aim of this thesis is to provide useful knowledge for pig breeding to be used in decisions on breeding goals and to improve genetic evaluation.

2 General background

2.1 Resource allocation and genetic correlations

Maintenance, growth, reproduction and survival are processes that require resources. These resources consist of food consumed, fat and protein reserves, and the physiological condition of the animal (Rauw, 2009). According to the resource allocation theory (Beilharz et al., 1993), different processes in the body compete for the resources available. For example, if more resources are used for reproduction there will be fewer resources left for maintenance and growth. Also within a process, resources are allocated to different parts of that process (Rauw, 2009).

The mechanisms for resource allocation are partly under genetic control with many gene interactions involved. Genetic correlations between traits are caused by pleiotropy or linkage disequilibrium. Pleiotropy is when one gene affects two or more traits and linkage disequilibrium is when genes are so closely located on the chromosome that it prevents the genes from segregating independently during meiosis. These genetic correlations between traits can either be favourable (give a desirable change in both traits) or unfavourable (give a desirable change in one trait and an undesirable change in another trait). Compared to wild animals, the resources for domestic animals are usually less limiting. This makes it possible to utilize the excess in forms of i.e. increased growth and reproduction. Through selection it is possible to change the amount of resources allocated to a specific trait and thereby profit from increased production. However, due to unfavourable genetic correlations between some of the traits in the same and/or different processes, the profit of selection for a desired trait will be lowered because of the costs for undesired changes in other traits.

2.2 Piglet growth

2.2.1 Litter heterogeneity and piglet growth

A good start early in the piglet's life, expressed as high growth rate, is the basis for further successful performance of the growing pig and young sow (Rydhmer et al., 1989). Already in the uterus, competition starts between the piglets for resources such as nutrients and space (Drake et al., 2008). Differences in body weight between individuals within the same litter are accentuated after birth, when the competition for resources, such as milk, continues. Under these conditions, larger piglets are more efficient in gaining access to the udder than their smaller littermates (Pluske & Williams, 1988; Wolter et al., 2002). Heterogeneity is a problem mainly for piglets with low body weight which suffers from delayed growth (Foxcroft et al., 2006). In the pig industry, the lack of uniformity in body weight within litters is a concern because it is likely to affect the ease of management of pigs in later stages of production, which may result in a loss of income for the farmer (Roberts & Deen, 1995).

Piglet growth is regulated by both the genes of the sow and the genes of the piglet. The genotype of the sow (maternal genetic effect) explains most of the genetic variation in birth weight (Hermesch et al., 2001; Arango et al., 2006). However, with the progression of lactation, the genotype of the piglet (direct genetic effect) accounts for an increasing proportion of the variation in piglet body weight (Kaufmann et al., 2000; Hermesch et al., 2001). Grandinson et al. (2005) estimated the direct and maternal effects for birth weight, daily weight gain from birth to weaning and from weaning to 9 weeks of age in a pure bred Yorkshire population. Their heritability estimates (direct and maternal) were 0.07 and 0.19 for birth weight, 0.13 and 0.16 for daily weight gain before weaning and 0.20 and 0.06 after weaning.

2.2.2 Milk production

Milk production increases with increased litter size, but milk intake per piglet decreases. The sow's milk production is reflected in the piglet weight gain through the relationship of 1 kg piglet live weight corresponding to about 4 kg milk (e.g. Noblet & Etienne, 1989). Piglets weigh around 1.5 kg at birth and are expected to grow up to about 10 kg at weaning (about 5 weeks in Norway and in Sweden) which corresponds to a daily growth rate of ~ 240 g. In the first

24 hours after farrowing the nursing frequency is about one every hour and it decreases over time during lactation (Algers, 1993; Valros et al., 2003). Piglets have a very high growth capacity and milk production becomes limiting from day 8 or 9 of lactation (Hurley, 2001). The milk production peaks between week 3 and 4 of lactation (Hurley, 2001). The difference between the piglets needs for expressing the full potential of growth and the milk production increases up to weaning. Lactation lengths differ between countries due to practice or laws/regulations. The lactation length in Norway, Sweden and Finland is 4-5 weeks. According to EU legislations, piglets should not be weaned before 28 days and in batch wise systems a lactation length of 21 days is allowed.

2.3 Feed intake, body condition and shoulder ulcers

Sows increase their feed intake during lactation to compensate for the negative energy balance caused by milk production, but usually not to a sufficient level. As a consequence there is a loss of body reserves up to the third week of lactation and thereafter the sow starts to recover (Revell & Williams, 1993). It has been shown, both at the phenotypic and genetic level, that sows with a higher ability to use their body reserves during lactation produce faster growing piglets with lower mortality risk compared to sows which mobilize less body reserves (Valros et al., 2003; Grandinson et al., 2005). At the same time as selection for large and heavy litters are progressing, with depletion of sows' body reserves at weaning as a consequence, the selection for leanness (de Vries & Kanis, 1994; Edwards, 1998) adds to the issue in at least two important ways. One is the genetic relationship between leanness and appetite resulting in leaner animals having lower appetite (Kanis, 1990). The other one is leanness per se, where leaner animals will have less body reserves already from the start of lactation.

2.3.1 Shoulder ulcers

Poor sow body condition at farrowing and during lactation increases the risk of developing shoulder ulcers (Davies et al., 1997; Bonde et al., 2004; Zurbrigg, 2006; Knauer et al., 2007). Shoulder ulcers appear when tissue is under pressure between a surface and the tuber of the scapular spine for a longer time, or repeatedly without enough time in between for the tissue to recover from the resulting ischemia (Jensen, 2009).

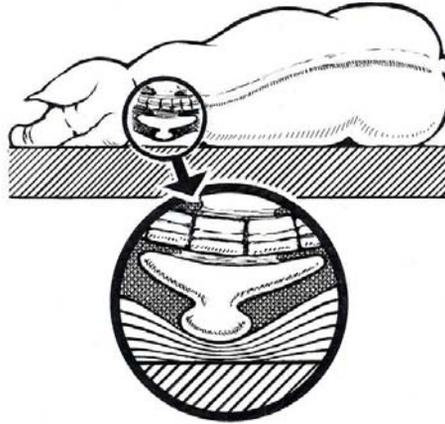


Figure 1. Graphical sketch of the shoulder blade and its pressure on the skin of a sow lying in lateral position (Vestergaard et al., 2005).

Shoulder ulcers in sows is a welfare problem (Broom, 1988; Herskin et al., 2010). These ulcers are believed to cause varying levels of pain in the different stages and they are also an entrance for pathogens causing infections (Herskin et al., 2010). As reviewed by Bonde et al. (2007), the etiology for shoulder ulcers is multifactorial. Environmental as well as more sow related factors influence the prevalence and severity of shoulder ulcers. It could for example be feeding routines, flooring, pen size, health status, shoulder ulcers in previous lactations and differences in the anatomy of the shoulder blade. The incidence rate of shoulder ulcers among sows in pig production varies between 10 and 34 % in studies based on farm data as well as on information from slaughter houses (Baustad & Fredriksen, 2006; Zurbrigg, 2006; Knauer et al., 2007; Bonde, 2008; Ivarsson et al., 2009; KilBride, 2009). Preliminary results from Swedish nucleus and multiplier herds indicate an incidence rate of 18% percent in Swedish Yorkshire sows (unpublished). Costs for shoulder ulcers are generated by treatments, reduced carcass value due to total or partial condemnation and replacement of culled sows with gilts (Gunnar Johansson, 2010, Swedish Animal Health Service).

2.4 Production and reproduction

Not only should the sow produce a large and heavy litter with equally sized piglets that grow fast and stay healthy. Moreover, this performance is expected to be repeated through consecutive parities. After weaning the litter, the sow is expected to show oestrus within a week. Based on the discussion by ten Napel (1996), weaning-to-service intervals (WSI) can be divided into normal (≤ 7 days) and prolonged (> 7 days) intervals. Sows with prolonged intervals will have a higher number of unproductive days and thereby increase the costs of piglet production. In addition, sows with increased WSI tend to produce smaller litters in the next parity (Tummaruk et al., 2000). In general, the genetic relationship between litter sizes of consecutive parities is favourable (e.g. Hermesch et al., 2000; Holm et al., 2005); sows with a genetic capacity to produce a large litter, i.e. many piglets, in 1st parity tend to produce large litters in the following parities as well. However, a reduced litter size (second litter syndrome, SLS) can occur in 2nd parity sows (Morrow et al., 1989) and this is related to body condition (Schenkel et al., 2010). Less is known about the genetic relationship between litter weight and reproductive performance in the following parities. Culling is the ultimate consequence for sows with unsatisfying reproductive performance. A large proportion of this culling takes place at low parity numbers (Engblom et al., 2007). For economic reasons, it is of great importance to the farmer to have sows with high annual productivity, achieved by sows that reproduce and produce well and remain in the herd in several parties (Engblom et al., 2007).

3 Aims of the thesis

The overall aim of this thesis is to provide knowledge for pig breeding to be used in decisions on breeding goals and to improve genetic evaluation. Breeding for increased piglet and litter weights without negative effects on the performance and welfare of the sows is of importance for sustainability; including economic, environmental and social aspects. The following hypotheses will be tested:

- There are unfavorable genetic relationships between the direct and maternal effects on piglet growth and between piglet growth and litter heterogeneity.
- There is a genetic variation in feed intake of the sow during lactation. This variation can be detected through simplified on-farm measurements for possible use in breeding programs.
- The association of piglet growth with the feed intake of the sow during lactation is expressed both on the phenotypic and the genetic scale.
- The genetic variation in sows' ability to make piglets grow is related to sows' metabolic status (feed intake and body condition) after farrowing.
- Shoulder ulcers in sows at weaning is a heritable trait. Selection for high piglet growth can deteriorate sow body condition at weaning and increase the risk of shoulder ulcers
- Selection for high piglet growth can affect the following reproduction cycle in a negative way.

4 Summary of studies

4.1 Material and methods

4.1.1 Material

Data were provided by the Norwegian pig breeding company Norsvin. Records and pedigree information were extracted from the Norwegian litter recording scheme. Data were mainly recorded in nucleus herds. A few multiplying and commercial herds (Paper II, III and IV) contributed with information on purebred Landrace animals. All recordings were done by the farmers or herdsmen. They were instructed by breeding technicians on how to judge appetite and score sow body condition, which were new traits introduced in this project. Data sets used for the studies in this thesis are presented in Table 1.

Table 1. *Information on data used in this thesis.*

	Paper I		Paper II	Paper III	Paper IV
	data set 1	data set 2			
Sows	981	9 475	15 946	5 549	4 606
Parities	1 – 4	1 - 4	1 - 2	1 - 8	1 - 2
Litters		14 045	11 323	7 614	4 123
Piglets	13 318	146 572	106 962		
Herds	5	58	74	45	39
Time period	2002 – 2005	2002 - 2007	2000 – 2007	2008 - 2010	2008 - 2010
sow data			2000 – 2007		
piglet data			2003 – 2007		

The pedigree for animals with records was traced five generations back when possible. In the studied herds, there was a 100% use of artificial insemination and the herds were genetically connected through the use of the same AI boars.

4.1.2 Traits

The studies compiled in this thesis included both normally distributed and categorical traits (Table 2). Normally distributed traits are continuous in their expression. The expression of categorical traits is in distinct classes, like normal/affected, and does not follow a normal distribution. However, the assumption is that the biology behind the trait follows a normal distribution. Shoulder ulcers, DELAYED and PREGNANT were analyzed as categorical traits. All other traits were considered as normally distributed.

Table 2. *Trait definitions and abbreviations used in the thesis*

Traits	Abbreviations	In Paper
Number of piglets born alive	NBA	I
Mean body weight at birth, kg	MBWB	I
Standard deviation in body weight at birth, kg	SDBWB	I
Mean piglet weight at 3 weeks, kg	MBW3/ meanW3	I/ II, III
Standard deviation in body weight at 3 weeks, kg	SDBW3	I
Individual body weight at 3 weeks, kg	BW3	I
Individual piglet weight gain at 3 weeks, kg	IWG03	II
Litter weight at 3 weeks, kg	LW	IV
Perception of sow appetite during 3 weeks from start of lactation, score 1-3 ¹	APP	IV
Sow feed intake at one day in the 3 rd week of lactation, MJ net energy/day	FEED	IV
Sow body condition score at weaning, score 1-9 ²	BC	III, IV
Shoulder ulcers, No=1/Yes=2		III
Weaning-to-service interval, 1 – 7 days	WSI7	II, IV
Weaning-to-service interval, 1 – 50 days	WSI50	II, IV
Inseminated within one week after weaning, Yes=1/No=2	DELAYED	IV
Pregnant on the first insemination after weaning, No=1/Yes=2	PREGNANT	IV
Number of piglets born in second parity	NBTnext/NBT2	II/IV

¹APP scores: 1=reduced, 2=normal and 3=very good

²BC scores: from very thin (1) to very fat (9)

Models

Different effects were included in the models used to estimate variance components (Table 3). In Paper I - III, animal models (with a direct genetic effect) were applied on all traits except for BW3 and IWG03 where both a direct and a maternal genetic effect were included. In Paper IV, animal or sire models were used depending on the trait combinations.

Table 3. *Effects included in the statistical models used in this thesis. As direct genetic effect, either animal (a) or sire (s) was used. For trait abbreviations, see table 2.*

	Fixed			Random							Covariates																		
	herd	year	season	herd-year	year-season	birth parity	parity	sex ratio	sex	piglet's age	herd-year	herd-year-season	permanent environment	litter	direct genetic	maternal genetic	residual	age at first service	age at first farrow.	no. born alive	no. born alive ²	age at 3 weeks	age at feed reg.	no. weighed	no. weaned	lactation length	lactation length ²	lactation length ³	
NBA			X				X	X		X	X	X		a		X													
MBWB			X				X	X			X	X		a		X				X									
SDBWB			X				X	X			X	X		a		X				X									
MBW3 ^x			X				X	X		X	X	X		a		X				X									
SDBW3 ^x			X				X	X		X	X	X		a		X				X									
BW3			X				X		X	X	X	X		a		X	X												
meanW3 (II)				X								X		a		X		X		X	X	X							
meanW3 (III)	X				X		X					X		a		X		X				X		X					
IWG03				X		X			X			X		a		X	X	X		X		X							
LW	X	X	X									X		a/s		X		X				X							
APP	X	X	X									X		a		X		X											
FEED	X	X	X									X		a/s		X							X						
BC (III)	X				X		X					X		a		X									X	X			
BC (IV)	X	X	X								X	X		a/s		X		X								X	X		
Shoulder ulcers	X				X		X					X		a		X									X	X			
WSI7 (II)				X								X		a		X		X									X		
WSI7 (IV)	X	X	X									X		s		X		X		X							X		
WSI50 (II)				X								X		a		X											X		
WSI50 (IV)	X	X	X									X		s		X											X		
DELAYED	X	X	X									X		s		X										X	X	X	
PREGNANT	X	X	X									X		s		X		X								X			
NBTnext (II)				X		X						X		a		X			X							X	X		
NBT2 (IV)	X	X										X		a		X										X	X		

4.1.3 Methods

To obtain significance levels and least squares (LS) means of fixed effects, the SAS software version 9.1 (SAS Institute Inc., Cary, NC, USA) was used. For all normally distributed traits, estimations were made with PROC MIXED. For the categorical traits shoulder ulcers (Paper III), DELAYED and PREGNANT (Paper IV), PROC GLIMMIX was used with a binary distribution and a logit link function.

Both likelihood and Bayesian methods were used in the statistical analyses of genetic parameters. In Paper I and II, genetic analyses were made by using the average information restricted maximum likelihood algorithm (AI-REML) developed by Jensen et al. (1997) in the DMU software (Madsen & Jensen, 2007). Standard errors of the heritability estimates were computed based on a first-order Taylor series expansion.

In Paper III and IV, analyses were performed using the Gibbs sampling algorithm with the programs THRGIBBS1F90 (Paper III and IV) and GIBBS2F90 (Paper IV) developed by Tsuruta and Misztal (2006). Flat priors were used and the Gibbs sampler was run as single chains with 500 000 (Paper III) and 2 000000 samples (Paper IV). The post-Gibbs analysis for Paper III was done using the program POSTGIBBSF90 (Misztal et al., 2002) and for Paper IV by using the program Gibanal version 2.8 (van Kaam, 1998).

4.2 Main findings

4.2.1 Heritability estimates

Both direct and maternal heritabilities were estimated. For formulas used when calculating the heritabilities as well as standard errors (SE) or posterior standard deviations (PSD) of estimates, see Paper I-IV.

Table 4. *Summary of heritability estimates in this thesis.*

For SE and PSD, see Paper I – IV.

Traits ¹	h^2_a	h^2_m
NBA	0.11	
MBWB	0.32	
SDBWB	0.10	
MBW3	0.18/0.17	
SDBW3	0.08/0.08	
BW3	0.03	0.07
meanW3	0.21/0.23	
IWG03	0.15	0.10
LW	0.22	
APP	0.07	
FEED	0.05	
BC	0.14/0.17	
Shoulder ulcers	0.25	
WSI7	0.08/0.12	
WSI50	0.03/0.14	
DELAYED	0.41	
PREGNANT	0.27	
NBTnext/NBT2	0.09/0.11	

¹ See Table 2 for trait definitions and abbreviations.

4.2.2 Genetic correlations

Estimates of genetic correlations are summarized in Table 5 – 6 (Paper I) and Table 7 (Paper II – IV).

Table 5. *Genetic correlation estimates (Paper I) with SE as subscript.*

Trait ¹	SDBWB	MBW3	SDBW3
MBWB	0.36 _{0.25}	0.60 _{0.16}	0.09 _{0.27}
SDBWB		0.48 _{0.26}	0.51 _{0.31}
MBW3			0.77 _{0.27}

¹ See Table 2 for trait definitions and abbreviations.

Table 6. *Genetic correlation estimates (Paper I) with SE as subscript.*

Trait ¹	BW3 _{maternal}	MBW3	SDBW3
NBA		-0.40 _{0.07}	-0.03 _{0.11}
BW3 _{direct}	-0.43 _{0.10}		-0.18 _{0.14}
BW3 _{maternal}			0.66 _{0.08}
MBW3			0.61 _{0.08}

¹ See Table 2 for trait definitions and abbreviations.

Table 7. Summary of genetic correlation estimates (Paper II – IV) with SE or PSD as subscript. Some of the estimates are presented as means. See Table 2 for trait definitions and abbreviations.

	IWG03 _{maternal}	LW	Shoulder ulcers	BC	WSI7	WSI50	DELAYED	PREGNANT	NBT2
IWG03 _{direct}	0.32 _{0.06}				0.23 _{0.14}	0.28 _{0.18}			0.18 _{0.12}
IWG03 _{maternal}					-0.01 _{0.11}	0.08 _{0.15}			-0.39 _{0.10}
meanW3			0.23 _{0.10}	-0.24 _{0.10}	0.04 _{0.13}	-0.07 _{0.17}			-0.37 _{0.12}
APP		0.61 _{0.16}		0.24 _{0.21}					
FEED		0.27 _{0.22}		0.52 _{0.20}	0.20 _{0.34}	0.33 _{0.30}	0.12 _{0.35}	0.33 _{0.35}	0.36 _{0.20}
LW				-0.54 _{0.15}	0.43 _{0.23}	0.33 _{0.21}	0.14 _{0.23}	-0.15 _{0.23}	0.29 _{0.17}
BC			-0.59 _{0.09}		-0.19 _{0.30}	-0.10 _{0.26}	-0.13 _{0.27}	0.18 _{0.27}	0.64 _{0.13}
WSI7									-0.03 _{0.16}
WSI50									0.10 _{0.20}

5 General discussion

Many genetic parameters are presented in this thesis. Significant estimates of correlations or not, piglet production *is* sow reproduction and no trait in this thesis is independent from the other traits, they are all directly or indirectly related. However, the discussion here will continue to follow the structure of the introduction. Own results will be compared to other studies and interpretations and suggestions for breeding will be presented. In the end, the intention is to bring together some of the pieces of the sow-piglet puzzle.

5.1 Piglet growth (Paper I)

5.1.1 Weight heterogeneity

The within-litter heterogeneity observed in piglet production is a consequence of the reproductive strategy of the pig as a species, having a large litter size but small piglets (Drake et al., 2008). The ovulation is extended over a time period where most of the follicles will be ready for conception earlier and a smaller fraction of the follicles will be developed later (Pope et al., 1990). There is competition between the embryos about the space and nutrients in the uterus and when the piglets are born the competition for resources continues (Drake et al., 2008). In this study, as in many others, the genetic capacity to produce large litters was related to lighter piglets at 3 weeks.

Piglets with higher birth weight will have higher weight until weaning and this phenotypic relationship will persist in the growing phase as well as in the development of the gilts (Rydhmer et al., 1989). The genetic correlation between mean weight at birth and mean weight at 3 weeks was positive and favourable in this study. Sows with the genetic capacity to produce litters with high mean piglet weight at birth also have the capacity to produce litters with high mean piglet weight at 3 weeks.

The genetic correlation between mean piglet weight at 3 weeks and the weight deviation (SD) of the litter at the same age was high and positive. Thus, sows with genetic capacity to produce litters with high mean piglet weight at 3 weeks are also prone to produce litters with high SD within the litter. The same pattern for mean weight and SD of the litter at birth and at 3 weeks was found by Damgaard et al. (2003). When separating the direct and maternal effect on piglet growth, it was found that the maternal effect on piglet weight at 3 weeks was positively correlated to SD in the litter. The corresponding genetic correlation between the direct effect and SD was negative, but not significant.

Optimizing feeding strategies during gestation could be important for production of more homogeneous, high quality piglets (Whittemore, 1996) This may also be beneficial for piglet survival. Including both direct and maternal effects of piglet weight together with the standard deviation of the litter could be another way of reducing litter heterogeneity.

5.1.2 Direct and maternal effects on piglet growth (Paper I and II)

The heritability estimates of both the direct and maternal effects on piglet growth were low. In Paper I, the direct heritability was lower than the maternal heritability. The opposite relation was found in Paper II. Kaufmann et al. (2000) estimated the direct heritability for weight at weaning (18-41 days of age) at 0.08 and the maternal heritability at 0.16. Grandinson et al. (2005) estimated the direct and maternal heritabilities for birth weight and daily weight gain from birth to weaning to 0.07 and 0.19 for birth weight, 0.13 and 0.16 for daily weight gain. In general, the maternal effect decreases with time as the piglets start to eat other feed than milk (Kaufmann et al., 2000; Hermesch et al., 2001; Grandinson et al., 2005).

The estimates of the correlation between the direct and maternal genetic effect on piglet growth were negative and unfavourable. There is an antagonistic relationship between the genetic capacity of the sow to produce heavy, fast growing piglets and the genetic capacity of the piglet to become heavy. This is in agreement with Grandinson et al. (2005) who estimated the genetic correlation between direct and maternal effects on piglet growth from birth to weaning to -0.30. An antagonistic relationship between direct and maternal genetic effects on weight traits has also been presented in other species (Huisman et al., 2008, Eriksson et al., 2004).

Due to the processes of conception and pregnancy the piglets are ‘ranked’ in birth weight from the start of life. Small piglets get less colostrum (Devillers et al., 2007) and they obtain less milk per suckle during the whole lactation (Campbell & Dunkin, 1982). The sow has no possibility to meet the demands of all her piglets to enable them to fully express their growth potential. Domestic pigs are selected for high growth rate but the piglets may be unable to show their genetic capacity for growth due to nutritional limitations before and after birth. This is most evident for the piglets ending up with a posterior teat, producing less milk than the anterior teats (Hurley, 2001). The smaller piglets, having to compete with their heavier littermates for resources, will gain less in weight than the heavier piglets (Drake et al., 2008).

In the genetic relationship between the direct and maternal effect on piglet growth, there is a clear trade-off: When selecting sows with the ability to raise fast growing piglets, we select against the piglets’ own ability for fast growth. It is therefore important to include both the direct and the maternal effects in the genetic evaluation of dam lines, and to select sire lines for increased piglet growth. It is also of importance to know about the relationships of both direct and maternal genetic effects and other traits, such as reproduction traits, to be able to balance negative consequences of selection.

5.2 Relationships between feed intake and body condition (Paper IV)

As described by Knap (2009), there has been an expressed concern during the last few decades about sows’ voluntary feed intake during lactation, increased demands on sows’ ability to build up and allocate body resources and the possible consequences on reproduction. However, there are few studies focusing on the genetic relationships in this area, especially studies using field data. Results from this study show that it is possible to detect genetic variation in sow appetite during lactation through simplified measures. The heritabilities for the feed intake traits were, however, lower (0.05 - 0.07) than previously reported in the literature, which may be explained by the trait definition. The appetite trait (APP) was the farmer’s perception of the animal’s appetite during the first three weeks of lactation and the feed intake trait (FEED) was the feed intake of only one day in week three after farrowing. In other studies, average feed intake of the whole lactation or a specific time period during lactation (Bergsma et al., 2008; Bunter et al., 2010; Hermesch et al., 2010) have been used.

Sow feed intake in early lactation is important for piglet performance throughout the lactation, as shown by Wallenbeck et al. (2008) and in Paper IV, where the phenotypic correlations between appetite and litter weight and between feed intake and litter weight were positive. The genetic correlation between appetite and litter weight was positive and favourable and the genetic correlation between feed intake and litter weight showed the same relationship. Sows with good appetite after farrowing and high feed intake at lactation peak are the ones with genetic potential for heavy litters. Bergsma et al. (2008) estimated a similar genetic correlation between voluntary feed intake during lactation and litter weight gain. However, one can assume a certain amount of autocorrelation between feed intake and litter weight in Paper IV. Despite a recommendation of *ad lib* feeding, the farmer is probably less motivated to follow that recommendation when a sow is raising a litter of less than ten piglets than when the sow raises a large litter.

In Paper IV, the genetic correlation between litter weight and feed intake tended to be positive (but with large PSD) and feed intake was favourable correlated to body condition. Thus, sows with genetic capacity for high feed intake are able to maintain a good body condition during lactation. Even so, the genetic correlation between litter weight and body condition is unfavourable which means that selection for heavy litters can result in low body condition at weaning. Only first parity sows were included in Paper IV. Such young sows are still growing (Solanes & Stern, 2001) and need a large feed intake to fulfil the high energy requirements during lactation. The results in Paper IV is in agreement with Eissen et al. (2000), who propose that voluntary feed intake during lactation should be included in the genetic evaluation.

5.3 Shoulder ulcers (Paper III)

Genetics of shoulder ulcers

The heritability estimate for shoulder ulcers (0.25 on the underlying scale) can be considered as a high value since the measure of the trait was relatively rough. Furthermore, we did not use all the available information from the recordings, since we used an affected/not affected approach in the analysis. The effect of environmental and biological factors on shoulder ulcers has been described by Davies et al. (1997), Cleveland-Nielsen et al. (2004), Bonde et al. (2004) and Rolandsdotter et al. (2009) but there are few reports on genetic parameters of shoulder ulcers in the literature (Bradley, 2005, Velandar & Nielsen 2011). Hedebro-Velandar et al. (2011) estimated the genetic

correlation between the body condition and the mean ulcer size per lactation to -0.23.

The sows in this study were purebred Norwegian Landrace sows. In a Canadian study, Landrace and Duroc sows were more likely to develop shoulder ulcers than Yorkshire sows (Zurbrigg, 2006). Breed combination in crossbred sows may affect the presence of shoulder ulcers (Bonde et al., 2007). Anatomical, physiological (e.g. stress response, immune response) and behavioural differences, could explain some of the variation in shoulder ulcers. Further studies of breed effects on shoulder ulcers could be interesting for the pig industry.

Body condition and litter size

Sows with poor body condition have an increased risk of developing shoulder ulcers. This fact is well documented on a phenotypic level (Davies et al., 1997; Bonde et al., 2004; Zurbrigg, 2006; Knauer et al., 2007; Ivarsson et al., 2009). The genetic correlation between shoulder ulcers and mean piglet weight was unfavourable. Thus a genetic ability to raise heavy piglets increases the risk of shoulder ulcers. This is in agreement with the phenotypic study by Zurbrigg (2006). Hedebro-Velander et al. (2011) estimated the genetic correlation between the body condition and the mean ulcer size per lactation to -0.23.

There was a significant phenotypic effect of litter size at weaning on shoulder ulcers. Litter size is lower in 1st parity sows than in later parities and 1st parity sows had less shoulder ulcers in our study. However, the incidence of shoulder ulcers from 1st parity sows was significantly lower compared to older sows even after correction for litter size. This could be related to the fact that older sows raise heavier piglets, or maybe to aging in itself or longer exposure to unfavourable environmental effects. Ivarsson et al. (2009) reported that the development of shoulder ulcers increased from 4th to 5th lactation week. Also in Paper III, there was a significant effect of lactation length on the incidence of shoulder ulcers. Since the rather long lactation length used in Sweden and Norway is favourable for the piglets, it would be interesting to study more specifically when the shoulder ulcers appear and the effect of lactation length.

Welfare in breeding programs

In all Scandinavian countries, shoulder ulcers is a large part of the sow welfare discussion and action plans against shoulder ulcers have been developed (Ministry of Food, Agriculture and Fisheries, Denmark; Animalia, Norway;

Swedish Animal Health Service, Sweden). In Paper III, focus was on estimating genetic parameters for shoulder ulcers but the long-term aim is to decrease the frequency of shoulder ulcers by selection. If shoulder ulcers should be included in the genetic evaluation the trait must have an economic weight. Economic costs of treatments, extra work and extra replacement of sows and loss of carcass value can be calculated, but the costs of low pig welfare and possible losses due to consumers' mistrust in pork production are more difficult to predict (Olesen et al., 2000). If more weight is put on traits important for sow welfare the progress in production traits will slow down (Gourdine et al., 2010) and this cost should also be taken into account. One way forward is to define an economic weight by the desired-gain approach, as suggested by Kanis et al. (2005). In the first step, this desired gain could be no further deterioration of shoulder health. In addition, selection for robust pigs in general may decrease the risk of shoulder ulcers, since shoulder ulcers are more common in sows with health problems (Bonde et al., 2004; Knauer et al., 2007, Ivarsson et al., 2009). Both inferior health and stress may increase the time sows spend lying down (Bonde et al., 2007) and increased time lying down increases the risk of developing shoulder ulcers (Rolandsdotter et al., 2009). Due to the close relationship between shoulder ulcers and sow body condition, including body condition in the genetic evaluation could be an alternative.

5.4 Production and reproduction

5.4.1 Weaning-to-service interval (Paper II and IV)

Since the ability to show oestrus and become pregnant after weaning is crucial for the sow to remain in the herd, we focused on the sow's genetic ability to raise heavy litters and her genetic ability for reproductive capacity after weaning the 1st litter. The heritabilities estimated for delayed oestrus (mated > 7 days after weaning) and ability to become pregnant were high. If comparing with estimates in the literature (e.g. Rydhmer, 2000), it should be remembered that the heritabilities in Paper IV were estimated with a threshold model, and they had large PSD. Anyway, including PREGNANT in the genetic evaluation should be considered, since each failure results in a loss of three weeks. All data needed for including this trait are already present in most data bases.

Negative energy balance has a negative influence on reproduction hormones (e.g. luteinizing hormone) important for the development of follicles (Whittemore, 1996). When producing large and heavy litters, the depletion of

body reserves increases the risk for a delayed oestrus after weaning. Sterning et al. (1990) found an unfavourable phenotypic correlation between litter weight gain and days from weaning to oestrus of 0.18.

In Paper IV, the phenotypic correlation between litter weight and weaning-to-service interval was 0.08. Our hypothesis was that also the genetic correlation between litter weight and WSI would be unfavourable. In study IV there was support for such a relationship (but it should be remembered that the estimates had large PSD). The corresponding correlations between these intervals and mean piglet weight and piglet growth in study II were close to zero. Litter weight describes the sow's milk production better than mean piglet weight and piglet growth, especially since the latter two were corrected for litter size (Paper II). Thus, the unfavourable relationship found in Paper IV should be taken as a warning; sows with genetic capacity for high litter weight at weaning may have a longer WSI.

The genetic correlations between body condition and WSI and having a prolonged interval (DELAYED) were favourable but with large PSD. Estimates between the same traits reported by ten Napel et al. (1998) were close to zero. The genetic correlation between body condition and the ability to get pregnant on the first insemination was favourable, but also this estimate had a large PSD. Similar relationships have been reported for cattle (Berry et al., 2003)

Tummaruk et al. (2000) reported that a prolongation of WSI from 4 to 10 days decreases the number of piglets produced in the next litter. Poleze et al. (2006) also found this negative effect of the interval from weaning to oestrus (IWO) on litter size in the subsequent litter. In Paper II, the phenotypic correlation between WSI and litter size in the 2nd parity was close to zero. The genetic correlation was negative, but not significant.

5.4.2 Litter size (paper II and IV)

Quesnel et al. (2007) showed that sows with high milk production due to large litters mobilized more body reserves, which affected the development of follicles after weaning. The average volume of the 14 largest follicles 3 days after weaning was lower in sows nursing large litters (13-14 piglets) as compared to sows nursing small litters (7 piglets). The sow has limited ability to compensate for the increased demand of energy by increasing feed intake. Eissen et al. (2000) emphasized the importance of a high feed intake; the lactating sow cannot eat enough to fully meet the requirements. An

unsatisfying, low feed intake affects reproductive hormone levels, such as luteinizing hormone and follicle-stimulating hormone, and follicular growth during lactation (Kauffold et al., 2008).

Most sows in this study apparently had enough body reserves left after lactation to produce the hormones needed for onset of oestrus; 86% (Paper II) and 90% (Paper IV) of the sows with records on WSI were able to show oestrus within 7 days after weaning.

In the study presented in Paper II, many sows seem to fail to maintain a large litter size in the following parity since the genetic correlation between mean piglet weight and litter size in 2nd parity was negative and unfavourable. This was also the case for the genetic correlation between the maternal effect on piglet growth and litter size in 2nd parity. Hermesch et al. (2000) and Tholen et al. (1996) also presented a negative genetic correlation between the litter weight at 21 days in 1st parity and number born alive in the 2nd parity. Tholen et al. (1996) estimated this correlation at -0.45 and the correlation was similar from 2nd to 3rd parity ($r_g = -0.38$). Sows with genetic capacity to produce fast growing, heavy piglets in 1st parity may thus produce fewer piglets in the 2nd parity. In Paper IV, in contradiction to the results presented above, a positive genetic correlation between litter weight and number of piglets born in 2nd parity was found, but the estimate had a large PSD.

The genetic correlation between body condition at weaning and total number of piglets born in 2nd parity was positive and favourable. Sows with genetic capacity for high body condition at weaning may thus produce more piglets in 2nd parity. The estimated phenotypic correlation between these traits was around zero. Schenkel et al. (2010) reported LS means for second litter size of sows grouped in different categories in a number of body condition traits measured at weaning of the 1st litter. For the trait body condition, sows with high scores had more piglets in 2nd parity.

5.5 Recommendations for breeding

To maintain a good body condition is central for sow performance in piglet production. The aim is to produce many, heavy, high quality piglets at weaning. But high piglet and litter growth have a negative effect on sow body condition at weaning. Moreover, sows with low body condition have a larger risk of shoulder ulcers and they may produce less piglets in the

following litter. A too high selection pressure on body condition at weaning could, however, result in lower milk production due to reduced mobilization of body resources. Sows with high feed intake will have better possibilities to meet the demand for milk from the piglets without losing too much body reserves. Even if selection for improved sow performance in piglet production is important, further development of management and feeding routines is also necessary to provide the environment needed for the sows to be able to express their genetic potential.

In this thesis, focus was on the genetics of piglet growth, lactation feed intake, body condition, shoulder ulcers and reproduction. Figure 2 is an attempt to illustrate the complexity of these traits. It is important to have this complexity in mind when defining the breeding goal and choosing the selection traits, as well as when deciding the economic weights in a breeding program.

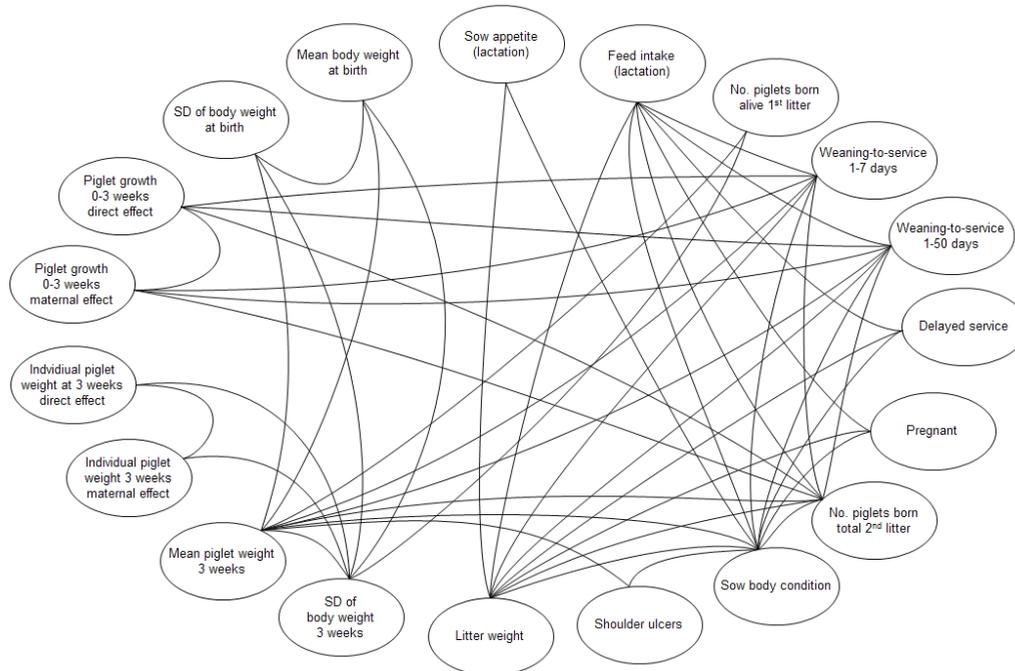


Figure 2 Studied relationships between traits in this thesis.

Despite the title of this thesis, it is impossible to cover all the genetic aspects of sow performance in piglet production in one PhD project. Piglet survival, behaviour of sows and piglets, rearing of gilts and longevity are other important issues to focus on. Even so, this thesis should motivate some changes of the current pig breeding. Based on the results, the following can be recommended:

- Record the identity of piglets together with data on biological and nursing mother, date of cross fostering and date of death, so that direct and maternal effects on piglet growth and survival can be estimated.
- Record individual piglet weight at 3 weeks, include both direct and maternal genetic effects in the genetic evaluation, and monitor genetic change in weight heterogeneity.
- Record sow body condition at weaning and include sow body condition in the genetic evaluation (together with the maternal ability to raise large and heavy litters), in order to decrease the risk of shoulder ulcers and increase the sows' reproductive capacity.
- Include the ability to get pregnant as a trait in the genetic evaluation, in order to improve reproductive performance and longevity.

The complexity illustrated in figure 2 is a challenge, but also an asset; the pig is amazing! Through well-developed breeding programs it is possible to achieve a sustainable piglet production.

6 Conclusions

The main conclusions to be drawn from the outcome of this project are as follows:

- There is an unfavorable genetic relationship between the maternal and the direct effect on piglet growth, and between the maternal effect on piglet growth and litter heterogeneity. Likewise, breeding for increased mean piglet weight could increase weight heterogeneity in the litter.
- It is possible to detect genetic variation in sow appetite and feed intake during lactation recorded in nucleus herds, but simple on-farm measurements of lactation feed intake needs to be further developed before they are used in breeding programs.
- The relationship between litter weight and feed intake of the sow during lactation (high feed intake – high litter weight) is expressed both on the phenotypic and genetic scale.
- The variation in sow's ability to make piglets grow is related to sow's metabolic status (feed intake and body condition) after farrowing. Sows with a genetic ability for high feed intake also have the ability to raise heavy litters. Thus, high feed intake during lactation is an important trait in piglet production. Moreover, a heavy litter is genetically related to a poor body condition of the sow at weaning.
- Shoulder ulcers in lactating sows is heritable and sows producing heavier piglets have a higher risk of developing shoulder ulcers compared to other sows. Due to the genetic correlations between

shoulder ulcers and mean piglet weight as well as sow body condition, it is important to take shoulder ulcers into account in breeding programs, in order to improve sow welfare and avoid associated economic losses.

- Selection for high piglet growth may deteriorate the sow's condition at weaning, which will affect the following reproduction cycle in a negative way. Selection for litter growth or piglet growth (as a sow trait) in 1st litter may prolong the interval from weaning to mating and decrease litter size in 2nd litter.

7 Future research

In this thesis, the genetic relationships between piglet growth traits in 1st parity and reproductive performance in 2nd parity were investigated in Paper II. In Paper IV, relationships with feed intake and body condition in 1st parity were added. In nucleus herds, where the ambition is to keep the generation interval as short as possible, most sows remain only for a few parities before they are culled due to low breeding values. What is further needed is knowledge about these relationships in higher parity numbers. The majority of the sows are producing in multiplier and commercial herds, where the economy is more dependent on the longevity of the sows. Future research on the consequences of selection for piglet growth should be performed on purebred sows in multiplier herds and on crossbred sows in commercial herds.

Selection for increased litter size has been successful and as a consequence, the number of piglets weaned is increasing. Nevertheless, levels of piglet mortality are not improving. A genetic progress in number of piglets weaned followed by increased piglet mortality ought to be questioned for ethical reasons. The public concern in this matter is illustrated by the fact that the Danish Ministry of Food, Agriculture and Fisheries recently ordered Danish researchers to write a report on piglet mortality (Pedersen et al, 2010). The genetic relationships between piglet mortality and sow body condition during the different reproduction phases (gestation, lactation and mating), as well as the impact of feeding strategies and management routines have to be studied further. Piglet survival is not a new research area, but today's negative trend emphasizes the need for future studies. A correct recording of the identity of all piglets, together with data on biological and nursing mother, date of cross fostering and date of death are a prerequisite for such studies.

8 Svensk sammanfattning

8.1 Bakgrund

I praktisk grisavel skiljer sig avelsmålen mellan faders- och moderslinjer. I avelsmålet för faderslinjer ligger fokus på produktion och avelsvärderingen innefattar egenskaper som till exempel tillväxt, köttighet och köttkvalitet. I avelsmålet för moderslinjer ingår förutom dessa produktionsegenskaper även reproduktionsegenskaper. Det finns ogynnsamma genetiska samband mellan produktions- och reproduktionsegenskaper, vilket ställer stora krav på avelsvärderingens utformning. Under de senaste decennierna har avelsarbetet i moderslinjerna fokuserat på ökad kullstorlek och smågristillväxt. Följaktligen ökar kravet på suggan att producera mer mjölk åt smågrisarna. Aveln för ökad kullstorlek och smågristillväxt pågår samtidigt med aveln för lägre fettansättning, vilket begränsar suggans möjligheter att lagra tillräckligt med kroppsreserver för den resurskrävande mjölkproduktionen. Dålig hullstatus och små fettreserver kan orsaka både reproduktionsproblem och välfärdsproblem.

Det övergripande syftet med detta doktorandprojekt var att generera kunskap som kan användas i utvecklingen av avelsmål och avelsvärdering för förbättrad prestation hos suggor och därmed ökad produktivitet i smågrisproduktionen.

8.2 Sammanfattning av studierna

Studierna i avhandlingen innefattar genetiska och fenotypiska analyser av data från det norska avelsföretaget Norsvin. I studierna ingick information om norska lantrassuggor och deras smågrisar. Lantbrukarna/djurskötarna utförde

alla mätningar och registreringar. De instruerades av Norsvins avelstekniker i att bedöma de nya egenskaperna hull, aptit och bogsår som introducerades i detta projekt. Alla de studerade besättningarna använde semin och djuren var genetiskt kopplade till varandra genom att samma semingaltar användes i flera besättningar.

I det här projektet studerades egenskaperna smågristillväxt och kullvikt, aptit och foderintag, hull, bogsår, intervall avvänjning-betäckning, förmåga att bli dräktig och kullstorlek. I avhandlingen presenteras arvbarheter och genetiska samband för dessa egenskaper. Det finns ett ogynnsamt genetiskt samband mellan den maternella effekten (suggans förmåga) och den direkta effekten (smågrisens förmåga) på smågristillväxt. Det finns också ett ogynnsamt genetiskt samband mellan den maternella effekten på smågristillväxt och viktspridningen i kullen. Det betyder att avel för ökad förmåga hos suggan att föda upp tunga smågrisar kan minska smågrisarnas tillväxtförmåga och öka viktspridningen i kullen.

Det är möjligt att med hjälp av enkla registreringar skatta den genetiska variationen i suggors foderintag under laktationen. Arvbarheten för denna egenskap var dock låg, vilket betyder att mätmetoden behöver utvecklas innan den används i avelsvärderingen. Vi fann både genetiska och fenotypiska samband mellan kullens totala vikt vid tre veckor och suggans foderintag under laktationen (högt foderintag - hög kullvikt).

Suggans förmåga att få smågrisarna att växa är genetiskt kopplad till suggans förmåga att utnyttja sina fettreserver under laktationen och därmed till hullet vid avvänjning (hög kullvikt – låg hullstatus). Bogsår hos digivande suggor är en ärftlig egenskap och suggor som producerar tunga smågrisar har en högre risk att utveckla bogsår jämfört med andra suggor. På grund av de ogynnsamma genetiska sambanden mellan bogsår och medelvikt hos smågrisarna samt mellan hull och bogsår är det viktigt att ta hänsyn till bogsår i avelsarbetet, för att förbättra välfärden och undvika ekonomiska förluster. Urval för hög smågristillväxt som leder till försämrad hullstatus hos suggan vid avvänjning kan också påverka den fortsatta reproduktionen på ett negativt sätt. Det kan yttra sig i längre intervall från avvänjning till betäckning och i lägre kullstorlek i nästa kull.

Ett gott hull är centralt för suggans produktivitet. Målet i smågrisproduktionen är att avvänja många, tunga och vitala smågrisar. Suggor med gott hull har en lägre risk att utveckla bogsår under digivningen och föder

fler smågrisar i nästa kull. Ett för högt selektionstryck på suggans hull vid avvänjning kan dock leda till lägre mjölkproduktion på grund av minskad mobilisering av kroppsreserver. Suggor med högt foderintag har bättre möjlighet att möta smågrisarnas efterfrågan på mjölk utan att förlora alltför mycket av sina egna kroppsreserver. Även om avel för mer produktiva suggor är viktigt, behövs ytterligare utveckling av skötsel- och utfodringsrutiner för att skapa en miljö där suggorna kan uttrycka sin genetiska potential.

Rekommendationer för praktiskt avelsarbete baserat på resultaten i denna avhandling:

Registrera smågrisarnas identitet tillsammans med uppgifter om både biologisk mor och fostermor, datum för ev. flytt till fostermor samt datum vid förekomst av smågrisdödlighet, så att direkta och maternella genetiska effekter på smågristillväxt och överlevnad kan skattas.

Registrera individuell smågrismvikt vid 3 veckor, inkludera både direkta och maternella effekter i avelsvärderingen och följ upp den genetiska förändringen i viktspridning inom kull.

Registrera suggans hull vid avvänjning och inkludera det i avelsvärderingen, tillsammans med suggans förmåga att föda upp en tung kull, för att minska risken för bogsår och öka suggans reproduktionsförmåga.

Inkludera förmågan att bli dräktig som en egenskap i avelsvärderingen, för att förbättra suggans reproduktionsförmåga och hållbarhet.

References

- Algers, B. 1993. Nursing in pigs: communicating needs and distributing resources. *J. Anim. Sci.* 71, 2826-2831.
- Arango, J., Misztal, I., Tsuruta, S., Culbertson, M., Holl, J.W., Heering, W. 2006. Genetic study of individual preweaning mortality and birth weight in large white piglets using threshold-linear models. *Livest. Sci.* 101, 208-218.
- Baustad, B.M., Fredriksen, B. 2006. Prevalence and prevention of decubital shoulder ulcers in Norwegian sows. Proc. Int. Pig Veterinary Society Congress, July 16-19, Copenhagen, Denmark.
- Beilharz, R.G., Luxford, B.G., Wilkinson, J.L. 1993. Quantitative genetics and evolution - Is our understanding of genetics sufficient to explain evolution. *J. Anim. Breed. Genet. - Z. Tierz. Zucht. Biol.* 110, 161-170.
- Bergsma, R., Kanis, E., Verstegen, M.W.A., Knol, E.F. 2008. Genetic parameters and predicted selection results for maternal traits related to lactation efficiency in sows. *J. Anim. Sci.* 86, 1067-1080.
- Berry, D.P., Buckley, F., Dillon, P., Evans, R.D., Rath, M., Veerkamp, R.F. 2003. Genetic relationships among body condition score, body weight, milk yield, and fertility in dairy cows. *J. Dairy Sci.* 86, 2193-2204.
- Bonde, M. 2008. Prevalence of decubital shoulder lesions in Danish sow herds (In Danish). Internal Report 12, University of Aarhus, Faculty of Agricultural Sciences, 8 pp.
- Bonde, M., Herskin, M.S., Jørgensen, E., Hjelholt Jensen, K. 2007. Knowledge synthesis of shoulder ulcers in sows (In Danish). DJF Husdyrbrug nr 81. Aarhus University, P.O. box 50, 8830 Tjele, Denmark
- Bonde, M., Rousing, T., Badsberg, J.H., Sørensen, J.T. 2004. Associations between lying-down behaviour problems and body condition, limb disorders and skin lesions of lactating sows housed in farrowing crates in commercial sow herds. *Livest. Prod. Sci.* 87, 179-187.
- Bradley, H. 2005. Variation in back conformation and prevalence of ulcers on the shoulders – a cohort study of related Swedish Landrace and Landrace*Yorkshire sows. Master Thesis, No. 270, Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences.
- Broom, D.M. 1988. The scientific assessment of animal welfare. *Appl. Anim. Beh. Sci.* 20, 5-19.

- Bunter, K.L., Lewis, C.R.G., Hermes, S., Smits, R., Luxford, B.G. 2010. Maternal capacity, feed intake and body development in sows. Proc. 9th World Congress on Genetics Applied to Livestock Production, August 1-6. Leipzig, Germany.
- Campbell, R.G., Dunkin, A.C. 1982. The effect of birth weight on the estimated milk intake, growth and body composition of sow-reared piglets. *Anim. Prod.* 35, 193-197.
- Cleveland-Nielsen, A., Bækbo, P., Ersbøll, A.K. 2004. Herd-related riskfactors for decubital ulcers present at post-mortem meat-inspection of Danish sows. *Preventive Veterinary Medicine* 64, 113-122.
- Damgaard, L.H., Rydhmer, L., Lovendahl, P., Grandinson, K. 2003. Genetic parameters for within-litter variation in piglet birth weight and change in within-litter variation during suckling. *J. Anim. Sci.* 81, 604-610.
- Davies, P.R., Morgan Morrow, W.E., Rountree, W.G., Miller, D.C. 1997. Epidemiologic evaluation of decubital ulcers in farrowing sows. *J. Amer. Vet. Med. Assoc.* 210, 1173-1178.
- de Vries, A.G., Kanis, E. 1994. Selection for efficiency of lean tissue deposition in pigs. In *Principles of Pig Science* (eds DJA Cole, J Wiseman and MA Varley), pp 23-41. Nottingham University Press, UK
- Devillers, N., Farmer, C., Le Dividich, J., Prunier, A. 2007. Variability of colostrum yield and colostrum intake in pigs. *Animal* 1, 1033-1041.
- Drake, A., Fraser, D., Weary, D. M., 2008. Parent-offspring resource allocation in domestic pigs. *Behav. Ecol. Sociobiol.* 62, 309-319.
- Edwards, S.A. 1998. Nutrition of the rearing sow and gilt. In *Progress in pig science* (eds J Wiseman, MA Varley and JP Chadwick), pp 361-382. Nottingham University Press, UK.
- Eissen, J.J., Kanis, E., Kemp, B. 2000. Sow factors affecting voluntary feed intake during lactation. *Livest. Prod. Sci.* 64, 147-165.
- Engblom, L., Lundeheim, N., Dalin, A.M., Andersson, K. 2007. Sow removal in Swedish commercial herds. *Livest. Sci.* 106, 76-86.
- Eriksson, S., Näsholm, A., Johansson, K., Philipsson, J. 2004. *Genetic relationships between calving and carcass traits for Charolais and Hereford cattle in Sweden.* *J. Anim. Sci.* 82, 2269-2276.
- FAO, 2009. The state of food and agriculture - livestock in the balance. [online] Available from: <http://www.fao.org/docrep/012/i0680e/i0680e00.htm>. [Accessed 2011]
- Foxcroft, G., Dixon, W.T., Novak, S., Putman, C.T., Town, S.C., Vinsky, M.D.A. 2006. The biological basis for prenatal programming of postnatal performance in pigs. *J. Anim. Sci.* 84, Suppl. E105-112.
- Gourdine, J.L., de Greef, K.H., Rydhmer, L. 2010. Breeding for high welfare in outdoor pig production: a simulation study. *Livest. Sci.* 132, 26-34.
- Grandinson, K., Rydhmer, L., Strandberg, E., Solanes, F.X. 2005. Genetic analysis of body condition in the sow during lactation, and its relation to piglet survival and growth. *Animal Science* 80, 33-40.
- Hedebro-Velander, I., Nielsen, B., Henryon, M.A., 2011. Genetic variation in shoulder ulcers in crossbred sows exists. *Proc. 62nd Annual Meeting of the European Federation of Animal Science*, August 29 – September 1. Stavanger, Norway.

- Hermesch, S., Jones, R.M., Bunter, K.L., Gilbert, H. 2010. Consequences of selection for lean growth and prolificacy of sow attributes. Proc. 9th World Congress on Genetics Applied to Livestock Production, August 1-6. Leipzig, Germany.
- Hermesch, S., Luxford, B.G., Graser, H.U. 2000. Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for Australian pigs 3. Genetic parameters for reproduction traits and genetic correlations with production, carcass and meat quality traits. *Livest. Prod. Sci.* 65, 261-270.
- Hermesch, S., Luxford, B.G., Graser, H.U. 2001. Estimation of variance components for individual piglet weights at birth and 14 days of age. *Proc. Assoc. Advmt. Anim. Breed. Genet.* 14, 207-210.
- Herskin, M.S., Bonde, M.K., Jørgensen, E., Jensen, K.H. 2010. Decubital shoulder ulcers in sows: a review of classification, pain and welfare consequences. *Animal*
doi:10.1017/S175173111000203X
- Holm, B., Bakken, M., Vangen, O., Rekaya, R., 2005. Genetic analysis of age at first service, return rate, litter size, and weaning-to-first service interval of gilts and sows. *J Anim Sci.* 83, 41-48.
- Huisman, A.E., Brown, D.J., Ball, A.J., Graser, H.U. 2008. Genetic parameters for bodyweight, wool, and disease resistance and reproduction traits in Merino sheep. 1. Description of traits, model comparison, variance components and their ratios. *Aust. J. Exp. Agric.* 48, 1177-1185.
- Hurley, W. L., 2001. Mammary gland growth in the lactating sow. *Livest. Prod. Sci.* 70, 149-157.
- Ivarsson, E., Mattson, B., Lundeheim, N., Holmgren, N. 2009. Shoulder ulcers – prevalence and risk factors (In Swedish). *Pig Rapport* Nr. 42.
- Jensen, H.E. 2009. Investigation into the pathology of shoulder ulcerations in sows. *Veterinary Record* 165, 171-174.
- Jensen, J., Mäntysaari, E.A., Madsen, P., Thompson, R. 1997. Residual maximum likelihood estimation of (co)variance components in multivariate mixed linear models using average information. *J. Ind. Soc. Agric. Stat.* 49, 215-236.
- Kanis, E. 1990. The effect of food intake capacity on production traits in growing pigs with restricted feeding. *Anim. Prod.* 50, 333-341.
- Kanis, E., de Greef, K.H., Hiemstra, A., van Arendonk, J.A.M. 2005. Breeding for societally important traits in pigs. *J. Anim. Sci.* 83, 948-957.
- Kauffold, J., Gottschalk, J., Schneider, F., Beynon, N., Wahner, M. 2008. Effects of feeding level during lactation on FSH and LH secretion patterns, and follicular development in primiparous sows. *Reprod. Domest. Anim.* 43, 234-238.
- Kaufmann, D., Hofer, A., Bidanel, J.P., Kunzi, N. 2000. Genetic parameters for individual birth and weaning weight and for litter size of large white pigs. *J. Anim. Breeding and Genetics* 117, 121-128
- KilBride, A.L., Gillman, C.E., Green, L.E. 2009. A cross sectional study of the prevalence, risk factors and population attributable fractions for limb and body lesions in lactating sows on commercial farms in England. *BMC Veterinary Research* 5, 30.
- Knap, P.W. 2009. Voluntary feed intake and pig breeding. In: Torrallardona, D., Roura, E. (Eds.), *Voluntary feed intake in pigs*. Wageningen Academic Publishers, Wageningen, pp. 13-35.

- Knauer, M., Stalder, K.J., Karriker, L., Baas, T.J., Johnson, C., Serenius, T., Layman, L., McKean, J.D. 2007. A descriptive survey of lesions from cull sows harvested at two Midwestern U.S. facilities. *Prev. Vet. Med.* 82, 198-212.
- Madsen, P., Jensen, J. 2007. An User's Guide to DMU. A package for analysing multivariate mixed models. Version 6, release 4.7. University of Aarhus, Faculty Agricultural Sciences, Dept. of Genetics and Biotechnology, Research Centre Foulum, Denmark.
- Misztal, I., Tsuruta, S., Strabel, T., Auvray, B., Druet, T., Lee, D.H. 2002. BLUPF90 and related programs (BGF90). Proc. 7th World Congress on Genetics Applied to Livestock Production, August 19-23. Montpellier, France.
- Morrow, W. E. M., Leman, A. D., Williamson, N. B., Moser, R., Pijoan, C., 1989. Improving parity-two litter size in swine. *J. Anim. Sci.* 67, 1707-1713.
- Noblet, J., Etienne, M. 1989. Estimation of sow milk nutrient output. *J. Anim. Sci.* 67, 3352-3359.
- Olesen, I., Groen, A.F., Gjerde, B. 2000. Definition of animal breeding goals for sustainable production systems. *J. Anim. Sci.* 78, 750-582.
- Pluske, J.R., Williams, J.H. 1988. Split weaning increases the growth of small pigs. Proc. Australian Society of Animal Production 17, 453.
- Poleze, E., Bernardi, M.L., Amaral Filha, W.S., Wentz, I., Bortolozzo, F.P. 2006. Consequences of variation in weaning-to-estrus interval on reproductive performance of swine females. *Livest. Sci.* 103, 124-130.
- Prunier, A., Soede, N., Quesnel, H., Kemp, B. 2003. Productivity and longevity of weaned sows. In: Pluske, J. R., le Dividich, J., Verstegen, M. W. A. (Eds.), *Weaning the pig*. Wageningen Academic Publishers, Wageningen, pp. 385-419.
- Quesnel, H., Etienne, M., Pèrè, M.-C. 2007. Influence of litter size on metabolic status and reproductive axis in primiparous sows. *J. Anim. Sci.* 85, 118-128.
- Rauw, W. M., 2009. Introduction. In: Rauw, W. M. (Ed), *Resource allocation theory applied to farm animal production*. CABI International, USA, pp. 1-21.
- Revell, D. K., Williams, I. H. 1993. Physiological control and manipulation of voluntary food intake. In: Batterham, E. S. (Ed.), *Manipulating pig production IV*, APSA, Werribee, pp. 55-80.
- Roberts, J., Deen, J. 1995. Conformance quality in pig production. *Comp. Cont. Educ. Pract. Vet.* 17, 1308-1311
- Rolandsdotter, E., Westin, R., Algers, B. 2009. Maximum lying bout duration affects the occurrence of shoulder lesions in sows. *Acta Vet. Scand.* 51, Article no. 44.
- Rydhmer, L., 2000. Genetics of sow reproduction, including puberty, oestrus, pregnancy, farrowing and lactation. *Livest. Prod. Sci.* 66, 1-12.
- Rydhmer, L., Eliasson, L., Stern, S., Andersson, K., Einarsson, S., 1989. Effects of piglet weight and fraternity size on performance, puberty and farrowing results. *Acta Agric. Scand.* 39, 397-406.
- Schenkel, A.C., Bernardi, M.L., Bortolozzo, F.P., Wentz, I. 2010. Body reserve mobilization during lactation in first parity sows and its effect on second litter size. *Livest. Sci.* 132, 165-172.

- Solanes, F. X., Stern, S., 2001. Estimated Mature Weights and Growth Curves for Large White Sows. *Acta Agric. Scand. Sect. A-Anim. Sci.* 51(2):142 – 147.
- Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., Rosales, M., de Hann, C. 2006. Livestock's long shadow – Environmental issues and options. FAO, Rome.
<http://www.fao.org/docrep/010/a0701e/a0701e00.HTM>.
- Sterning, M., Rydhmer, L., Eliasson, L., Einarsson, S., Andersson, K. 1990. A study on primiparous sows of the ability to show standing oestrus and to ovulate after weaning. Influences of loss of body weight and backfat during lactation and of litter size, litter weight gain and season. *Acta Vet. Scand.* 31, 227-236.
- ten Napel, J. 1996. Genetic aspects of intervals from weaning to estrus in swine. Landbouwniversiteit Wageningen (Wageningen Agricultural University), Wageningen Netherlands, 165 pp.
- ten Napel, J., Meuwissen, T.H.E., Johnson, R.K., Brascamp, E.W. 1998. Genetics of the interval from weaning to estrus in first-litter sows: correlated responses. *J. Anim. Sci.* 76, 937– 947.
- Tholen, E., Bunter, K.L., Hermes, S., Graser, H.U. 1996. The genetic foundation of fitness and reproduction traits in Australian pig populations .2. Relationships between weaning to conception interval, farrowing interval, stayability, and other common reproduction and production traits. *Aust. J. Agric. Res.* 47, 1275-1290.
- Tsuruta, S., Misztal, I. 2006. THRGIBBS1F90 for estimation of variance components with threshold-linear models. Proc. 8th World Congress on Genetics Applied to Livestock Production, August 13-18. Belo Horizonte, MG, Brazil.
- Tummaruk, P., Lundeheim, N., Einarsson, S., Dalin, A.M. 2000. Reproductive performance of purebred Swedish Landrace and Swedish Yorkshire sows: II. Effect of mating type, weaning-to-first-service interval and lactation length. *Acta Agric. Scand. Sect. A-Anim. Sci.* 50, 217-224.
- Valros, A., Rundgren, M., Spinka, M., Saloniemi, H., Rydhmer, L., Hulthen, F., Uvnaas-Moberg, K., Tomanek, M., Krejci, P., Algers, B. 2003. Metabolic state of the sow, nursing behaviour and milk production. *Livest. Prod. Sci.* 79, 155-167.
- van Kaam, J.B.C.H.M. 1998. Gibanal – analyzing program for Markov Chain Monte Carlo sequences, Version 2.8. Department of Animal Sciences, Wageningen Agricultural University, The Netherlands.
- Vestergaard, K., Christensen, G., Petersen, L.B., Wachmann, H., (2004). Afgangsårsager hos søer - samt obduktionsfund hos aflivede og selvdøde søer. *Landsudvalget for Svin, Danske Slagterier. Meddelelse*, (nr. 656) pp. 1-14.
- Wallenbeck, A., Rydhmer, L., Thodberg, K. 2008. Maternal behavior and performance in first-parity outdoor sows. *Livest. Sci.* 116, 216-222.
- Whittemore, C.T. 1996. Nutrition reproduction interactions in primiparous sows. *Livest. Prod. Sci.* 46, 65-83.
- Wolter, B.F., Ellis, M., Corrigan, B.P., DeDecker, J.M. 2002. The effect of birth weight and feeding of supplemental milk replacer to piglets during lactation on preweaning growth performance and carcass characteristics. *J. Anim. Sci.* 80, 301-308.
- Zurbriggen, K. 2006. Sow shoulder lesions: Risk factors and treatment effects on an Ontario farm. *Journal of Animal Science* 84, 2509-2514.

9 Acknowledgements

My PhD education and the work of this thesis were performed at the Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences (SLU). Financial support from the Swedish Farmers' Foundation for Agricultural Research (SLF) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas) is gratefully acknowledged. The SLU fund for internationalisation of postgraduate studies, Stiftelsen Svensk Grisforskning and the Royal Swedish Academy of Agriculture and Forestry (KSLA) have provided travel grants for participation in conferences. Norsvin (Dan Olsen, Solveig Kongsrud, Magnus Haandlykken, Signe Lovise Thingnes, Torunn Aasmundstad, Bjarne Holm, Anders Ofsti and Håvard Tajet) kindly provided the data for the studies and contributed with discussions and comments.

Sincere thanks to my main supervisor Lotta Rydhmer and my co-supervisors Katja Grandinson, Nils Lundeheim, Odd Vangen and Laurianne Canario for good collaboration, encouragement and support throughout my PhD education and thesis writing.

Thank you! to Kristina Andersson, Freddy Fikse, Birgit Zumbach and Jessica Franzén, who kindly contributed their expertise in the making of this thesis.

Big thanks to all co-workers at Hgen over the years, especially the administrative staff (Jörgen, Siw, Bian, Monica, Harriet, Helena, Stickan och Dan), the 'Pig corridor' (Britt, Lotta, Nisse, Linda, Anna, Helena, Ulla and Monica), the staff in the research herd and the supporting PhD group (especially Lina C, Sandra, Anne and Weronica).

The support from family and friends have been, and is, greatly appreciated. Tusentals kramar till Cano, Tigris and Mira – jag älskar er!