Genetic Aspects of Maternal Ability in Sows

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Abstract

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The purpose of this thesis was to gain knowledge about the genetic background of different aspects of maternal ability in sows. Today's selection for increased litter size at birth will put higher demands on the sow's ability to take care of her litter, and may cause problems with increasing piglet mortality and decreasing piglet growth. This motivates inclusion of a measure of maternal ability into the breeding goal. The studied traits are different measures of piglet mortality, piglet birth weight, piglet growth, sow behaviour and sow body condition. Both direct genetic effects and maternal genetic effects influenced traits measured on the piglet. The maternal effect was more important than the direct effect for all traits measured prior to weaning. Piglet birth weight was favourably genetically correlated to survival of live born piglets. However, we found unfavourable genetic correlations between stillbirth and birth weight of the piglet. This indicates that selection for increased birth weight is not a recommendable strategy to improve piglet survival at birth. We also conclude that a breeding programme aiming at improving both pre-weaning survival and pre-weaning growth should include both these traits, as we found indications of unfavourable genetic correlations between them. The sow's capacity for a high pre-weaning growth rate and a high survival rate in her litters was genetically associated with a greater loss of weight and backfat in the sow during lactation. A large loss of body reserves may increase the risk of reproductive problems. Low heritabilities, ranging from 0.01 to 0.08, were estimated for the sow behaviour traits: sow's response to a screaming piglet, sow's response to piglet handling, fear of and aggression towards the stockperson. A strong response to a piglet scream was genetically associated with a lower mortality rate, and a high fear response was genetically associated with a higher mortality rate. In conclusion, it seems possible to improve piglet survival rate through selection. However, selection for piglet birth weight is not a good strategy. Sow behaviour, for example fear of the stockperson, could be a possible selection criterion to improve piglet survival. Some attention needs to be paid to the sow's body condition during lactation when selecting for improved piglet survival and growth.

Keywords: swine, piglet mortality, growth, birth weight, sow behaviour, body condition, heritability, variances, maternal effects

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"'Hallo!' said Piglet, 'what are you doing?'
'Hunting' said Pooh.
'Hunting what?'
'Tracking something' said Winnie-the-Pooh very mysteriously.
'Tracking what' said Piglet, coming closer.
'That's just what I ask myself. I ask myself, What?'
'What do you think you'll answer?'
'I shall have to wait until I catch up with it' "

Winnie the Pooh, 1926

Contents

Appendix

Papers I-III

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Grandinson, K., Lund, M. S., Rydhmer, L. and Strandberg, E. 2002. Genetic parameters for the piglet mortality traits crushing, stillbirth and total mortality, and their relation to birth weight. *Acta Agric. Scand., Sect. A, Animal Sci.* 52: 167-173

II. Grandinson, K., Rydhmer, L., Strandberg, E. and Thodberg, K. 2003. Genetic analysis of on-farm tests of maternal behaviour in sows. *Livest. Prod. Sci.* In press.

III. Grandinson, K., Rydhmer, L., Strandberg, E. and Solanes, F. X. 2003. Genetic analysis of sow body condition during lactation, and its relation to piglet survival and growth. 200X. In manuscript.

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Introduction

Background

The purpose of modern pig production is to produce high quality meat at low costs. Efficient pig production depends on a number of factors such as a rapid growth rate and a high reproductive rate. Consumer demands for less fat has also resulted in strong selection for lean meat production over the last 30 years.

The number of piglets produced per sow and per year is the economically most important reproductive trait for the pig producer (Palmø, 1999), and often the only reproductive trait included in breeding programmes. Today, sows of the Swedish Landrace and Yorkshire breeds average 12 and 11 piglets born per litter, respectively (Quality Genetics, 2003). This can be compared with reports of an average litter size of 4-5 for the European wild boar (*Sus Scrofa*), the main ancestor of our domesticated pigs (Fernández-Llario, *et al.* 1999; Harris *et al.*, 2001). The largest litter sizes among pigs are seen in the Chinese breeds, known for their superior reproductive performance. For example, a mean litter size of 14 has been reported for the Meishan breed (Bidanel *et al.*, 1989).

Although litter size at weaning is the desired goal for pig producers, the number of piglets born, or the number born alive, is the selection trait chosen in most cases. The heritability is quite low, but several reports show that selection has been successful (Southwood and Kennedy, 1991; Johnson *et al.*, 1999; Tribout *et al.*, 2003). However, there are a number of problems, including increased piglet mortality, associated with selection for increased litter size at birth. A selection experiment by Johnson *et al.* (1999) showed that selection for increased litter size at birth led to undesirable correlated responses in piglet mortality. After 14 generations of selection, the selected line had significantly larger litters at birth, but also a higher stillbirth rate and a higher mortality rate before weaning. Similar results are reported from France in a recent report on the intensive selection on litter size in French Large White during the last decade (Tribout *et al.*, 2003). In agreement, Lund *et al.* (2002) estimated significant negative genetic correlations between litter size at birth and piglet survival from birth to weaning in Landrace sows.

Negative genetic correlations between litter size and survival rate decrease the efficiency of selection on litter size at birth. Moreover, high piglet mortality is an important welfare concern. Improving piglet survival is therefore highly motivated, both from an ethical and an economical standpoint. Recently, there has been an increasing interest in the possibilities for improving piglet survival and maternal abilities in sows. For example, the international breeding company TOPIGS is selecting a sire line on the piglets own capacity for survival (Knol and Leenhouwers, 2002). In Norway, the breeding company Norsvin has started recording several traits connected to maternal ability, such as piglet weights and farrowing problems (Norsvin, 2003).

The number of piglets successfully weaned by a sow, and their quality, depends on a number of different factors. Litter size at birth is influenced by, for example, ovulation rate and embryo survival. The farrowing process, for example farrowing length, is involved in determining the number of piglets born alive. In this thesis, focus will be on survival of piglets during the pre-weaning period. The number of piglets still alive at weaning is influenced by several factors, illustrated in Figure 1.

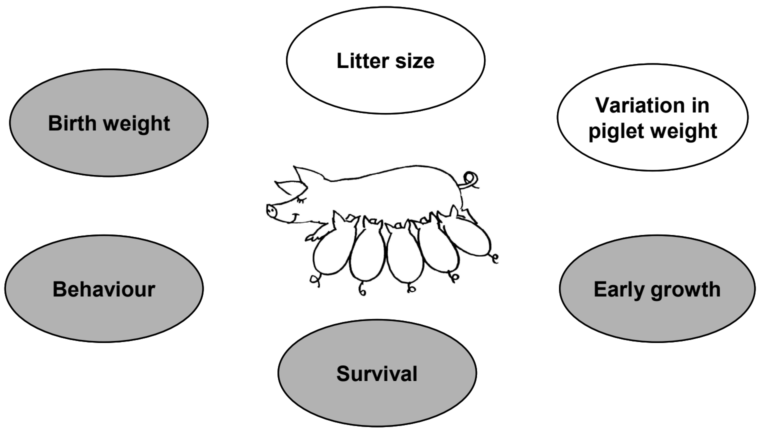


Figure 1. Examples of traits that can be used to measure good maternal ability in the sow. Traits regarded in this thesis are marked in grey.

The sow's behaviour is one component of maternal ability that has a very large influence on piglet survival. The sow faces a challenging task in successfully ensuring her offspring survive. The large number of offspring and the considerable size difference between the sow and the newborn piglet makes careful behaviour on the sow's part vital, to minimize the risk of crushing. Because a newborn piglet has very little energy reserves, it depends on the sow's milk for energy soon after birth. Milk production and nursing behaviour influence survival rate among piglets (English and Smith, 1975).

Maternal behaviour differs greatly between individual sows (Fraser, 1990). This individual variation is caused partly by environmental factors and partly by genetic factors. If there is large genetic variation in behaviour traits related to maternal ability, then selection for improved behaviour could be a means to improve piglet survival. However, very few genetic studies of maternal behaviour in sows have been performed.

In a farrowing pen, the sow is prevented from performing many of the behaviour patterns observed in sows under free ranging conditions. However, the motivation of sows to perform these behaviour patterns has not been changed through the process of domestication (Gustafsson *et al.*, 1999). The sow's motivation to perform certain behaviour patterns may still influence the chances of survival for her litter, even in an intensive commercial housing system (Fraser *et al.*, 1995). Therefore, when studying maternal success in domestic sows, it is important to understand the sow's behaviour in an un-restricted environment. The following paragraphs provide a short description of maternal behaviour observed in sows under free-range conditions. This is followed by a description of causes of piglet mortality, some behaviour traits affecting survival in sows housed indoors, and finally some aspects on piglet growth.

Maternal behaviour of sows under free-range conditions

Nest building

The wild boar and feral pigs live in small groups of often closely related females such as sisters and their daughters. Shortly before farrowing the sow leaves the family group and heads out for a long excursion to find a place where she can build a nest and farrow. The nest is built within 24 hours before farrowing. A sow can travel for distances well over 6 km to find a suitable nest-site. During this travel, she performs investigating behaviour, such as sniffing and rooting. Sows usually pick a well-protected place for their nests such as at the foot of a slope or under a tree. To construct the nest, the sow begins by making a shallow hole in the ground using her snout. She then gathers bedding material such as leaves and grasses from the surrounding area. When the nest is ready, the sow covers it with branches and digs herself into the nest and lies down (Jensen, 1986).

The nest provides insulation and protection for the newborn piglets (Haskell and Hutson, 1994). It also keeps the litter close to the sow, and thus may encourage mother-offspring bonding. Location of the nest away from the family group protects the piglets from being trampled by other adults and prevents older unrelated piglets from stealing milk from the sow (Jensen, 1989).

The nest occupation period

Normally, the sow does not leave the nest during farrowing. Most sows seem to get up at least once, usually in the beginning of farrowing. When standing, she turns around sniffing the piglets and then lies down again, typically in the opposite direction in the nest than before getting up. Before lying down the sow roots around the nest with her snout, removing piglets so she does not lie down on them. Towards the end of farrowing, the sows are quieter and seldom sit or stand (Petersen *et al.*, 1990).

The sow stays isolated from the family group until the piglets are about ten days old. During the farrowing day and the day after, both the sow and the piglets remain in the nest. Thereafter the sow leaves the nest to forage nearby. Within another day or two, the piglets follow her on shorter excursions around the nest. The sow moves further from the nest during the 2-5 days after farrowing and the piglets often return to the nest on their own (Jensen, 1986; Jensen and Redbo, 1987). The communication between sow and piglet also seems to change over time, from more nasal contact in the first days after farrowing to more acoustic signals in the last part of the nesting period. In the days before leaving the nest, the sow uses a “long grunt”, which appears to be a signal to the piglets to gather around her (Jensen and Redbo, 1987).

Integration of the litter with the family group

Once the nest is abandoned and the litter follows the sow back to the family group, they do not return to the nest again. The new litter is integrated gradually into the family group as the sow picks new resting places closer and closer to the family group (Jensen, 1986). During the first weeks after leaving the nest, the piglets have a high frequency of social interactions, but they tend to stay close to their own littermates and mother (Petersen *et al.*, 1989). As they grow older, the piglets also gradually increase the average distance they will move from their mother. The introduction of a new litter in the family group is uneventful, without aggression (Jensen, 1986; Petersen *et al.*, 1989).

Piglet mortality

Piglet mortality is often very high in pig production. In many production systems, up to 20 % of piglets born alive die during the pre-weaning period (*e.g.* Edwards *et al.*, 1986). Piglet mortality usually occurs within the first week, and even the first couple of days, after birth. Piglets with a low birth weight are more prone to die, especially if they are born in a large litter (Edwards *et al.*, 1986).

The three most common causes of pre-weaning death in piglets are stillbirth, starvation and crushing by the sow (English and Smith, 1975; Glastonbury, 1977; English and Morrison, 1984; Dyck and Swierstra, 1987). For stillborn piglets, the majority die during delivery due to oxygen deprivation (Glastonbury, 1977). The incidence of stillborn piglets increases if farrowings are long, and the risk of dying during the farrowing process increases for the piglets born late in the farrowing (Fraser *et al.*, 1995). Leenhouwers *et al.* (1999) showed a positive relationship between the number of stillborn piglets and the number of liveborn piglets that died before weaning, indicating that in litters with a high incidence of stillbirths there is an overall lower viability also of liveborn piglets.

It is often very difficult to assess the true cause of death. Many times piglets die because of a complex set of circumstances; for example, a crushed piglet may first have been weakened by malnutrition. Thus, these two major causes of death of liveborn piglets, crushing and starvation, are not mutually independent (English and Smith, 1975; Wechsler and Hegglin, 1997).

When not differentiating between crushed piglets that were viable before getting caught under the sow and those that were already weakened, crushing will often tend to be the major cause for pre-weaning mortality (*e.g.* Edwards *et al.*, 1986). English and Smith (1975), on the other hand, only classified piglets that appeared to have been viable and healthy as crushed. They considered weak piglets crushed by the sow to have died primarily because of starvation, making starvation the major cause of death. In many cases, crushing and starvation are just different outcomes of the same process. A piglet that is unable to receive enough milk will become weaker and will be at a greater risk of being crushed, but if it does not get crushed it will most likely starve to death (Fraser, 1990).

Crushing of healthy, viable piglets is related to the behaviour of the sow and how the sow responds to a piglet’s distress call. Crushing of already weak piglets that have been starved or injured does not have a similar correlation to the sow's behaviour (Wechsler and Hegglin, 1997). Starved piglets run a higher risk of being crushed partly because they are weaker and may as a consequence not be fast enough to get away from the sow. Piglets with low weight gain also tend to stay closer to the sow than other piglets to improve their access to the teats during nursing. Therefore, they spend more time in 'high-risk' areas compared to normal weight piglets (Weary *et al.*, 1996a). Inability to obtain an adequate amount of food can be due to a number of reasons. Some of these are related to the piglet's success, or rather lack of success, in competing with its littermates and some are related to traits of the sow such as low milk production or too few functional teats.

Some behaviour traits related to piglet mortality

Mortality is not randomly distributed over all litters. Instead, there are many litters with a large number of deaths, many litters with no deaths, and few with a moderate number of deaths. This indicates that some litters are more likely to have high mortality than others (Fraser, 1990). Large individual differences have been found in sow behaviour around and after farrowing, indicating that some sows are more likely to put their offspring at a risk of crushing and starvation, for example (Hutson *et al.*, 1991; Wechsler and Hegglin, 1997).

Pre-parturient behaviour

As described previously, the last 24 hours before farrowing are characterised by a high level of activity in free-ranging sows. Sows housed indoors, in pens or in crates also perform nest-building behaviours, such as rooting, nosing and pawing on the floor (Widowski and Curtis, 1990; Haskell and Hutson, 1996), even when no nest building material is available (Signoret *et al.*, 1975).

Providing sows with relevant stimuli for nest building can improve maternal behaviour. Sows given access to nesting material such as straw, sawdust or sand are more active prior to farrowing, but more passive once farrowing has started. This decreases the risk of crushing newborn piglets during parturition (Cronin *et al.*, 1993; Thodberg *et al.*, 1999). In addition, there are fewer intra-partum stillborn piglets (Cronin *et al.*, 1993), shorter parturition times (Cronin *et al.*, 1994), higher responsiveness to piglet distress calls (Cronin and van Amerongen, 1991; Herskin *et al.*, 1998), increased duration of suckling and decreased number of suckling sessions terminated by the sow (Herskin *et al.*, 1999). Cronin and van Amerongen (1991) were also able to show a lower death rate from birth to weaning for sows with the opportunity to build nests.

Behaviour related to crushing

Different movement patterns

Risk of crushing occurs when the sow changes body position, for example from standing to lying or from sitting to lying (Fraser, 1990). Fraser (1990) differed between two different movement patterns leading to either 'posterior crushing' or 'ventral crushing'. Posterior crushing may occur when the sow lies down from a standing position and piglets are trapped under her hindquarters. Ventral crushing occurs when the sow lies down from a sitting position and piglets are caught under her thorax. Posterior crushings are more common in loose-housed sows, whereas ventral crushing mostly occurs in crates (Fraser, 1990). There seems to be large individual differences in how sows behave when changing body position. Some sows are generally more careful than others when lying down (Blackshaw and Hagelsø, 1990; Wechsler and Hegglin, 1997).

McGlone and Morrow-Tesch (1990) reported that the time sows spend in a sitting position was positively correlated to the number of piglets crushed. Not all sows display sitting behaviour. Sows that showed no sitting behaviour had significantly lower number of piglets crushed than sows who did show sitting behaviour (McGlone and Morrow-Tesch, 1990). McGlone *et al.* (1991) proposed that if selection were performed against sitting behaviour, mortality through crushing would decrease. They found a heritability of 0.4 for sitting frequency in slaughter pigs, indicating that successful selection could be performed.

Rolling movements such as when a sow goes from lying on the udder to lying on the side also put piglets at risk for crushing. The danger of this movement seems more related to the speed and manner in which it is performed, than with the frequency with which it occurs. Rolling movements that crush piglets tend to be performed more quickly compared to rolling movements that do not crush piglets (Weary *et al.*, 1996b).

Crushing is more likely to occur when the sow lies down quickly (‘flops straight down’) from a standing position (Blackshaw and Hageslø, 1990; Wechsler and Hegglin, 1997) without first rooting around on the floor to remove piglets (Blackshaw and Hageslø, 1990; Marchant *et al.*, 2001). Wechsler and Hegglin (1997) showed that sows that never displayed the ‘flopping straight down’ manoeuvre had the lowest number of piglets trapped under them, and therefore fewer piglets were at risk of being crushed. Careless lying down behaviour, as well as sitting behaviour, could be related to leg problems. Good leg conformation of sows should help reduce the risk of crushing.

Responsiveness to distress calls from the piglet

Because sows and piglets are confined in a small space during the lactation period, there is an obvious risk that even a careful sow sometimes will lie down on her piglets. When this happens, the piglet could be saved if the sow responds to vocal and tactile stimuli from the piglet by standing up. When a piglet is caught under a sow, the risk of dying increases with the time the piglet remains trapped under the sow’s body (Weary *et al.*, 1996b).

There are large individual differences in how strongly a sow reacts to a piglet screaming and to other stimuli from the piglet. Some sows appear to be completely unaffected by the fact that they are lying on a screaming piglet while others are very alert, reacting by sitting or standing, letting the piglet escape (Hutson *et al.*, 1991). Sows who respond strongly to the sound of a screaming piglet seem to display less risky behaviour early postpartum (Thodberg *et al.*, 2002; Wechsler and Hegglin, 1997) and have fewer crushed piglets (Wechsler and Hegglin, 1997). There are, however, no reports of genetic studies on response to a piglet scream.

Fear and aggressive behaviour

Fear of humans

During their life, most production animals are handled frequently by humans during their life. Pigs are often exposed to close interaction with the stockperson. Sometimes these interactions are of a positive nature, for example a gentle stroke, but they can also be negative such as pushing or hitting. Regular human interactions can have large effects on behaviour, physiology and production of the animal (Hemsworth and Coleman, 1998).

Pigs that are exposed repeatedly to negative handling will start to avoid human contact and show increased levels of the stress hormone cortisol. These are indications of higher levels of fear. Several studies have shown that high levels of fear are related to decreased growth rates (Hemsworth and Coleman, 1998). A high level of fear in young gilts seems to be negatively associated with mating rates (Hemsworth *et al.*, 1990), and sows showing high levels of fear had higher stillbirth rates (Hemsworth *et al.*, 1999).

Hemsworth *et al.* (1989) found that variation in fear of humans in pigs accounted for 20% of the variation in reproductive performance across farms. But there are also individual variations between animals in how they respond to human interaction. Hemsworth *et al.* (1990) estimated a moderately high heritability for the trait "fear of humans" in young gilts, whereas avoidance of humans in sheep has been shown to have low heritability (Lambe *et al.*, 2001).

These results indicate that fear responses could be changed by selection, and this may have positive effects for production and reproduction traits. Hansen (1996) showed that selection for fear-related behaviour in mink markedly changed the behaviour of the animals in the selected line, so that they consistently responded aversively to human contact. However, there are very few studies of the genetic relation between fear behaviour and maternal success.

Aggression towards humans

Aggressive behaviour towards stockperson may be associated with a high level of maternal protectiveness that in turn could be related to good maternal behaviour. It is a common belief among farmers that more aggressive sows are also the better mothers. However, studies on aggression towards the stockperson have shown no evidence for such an association with piglet survival (Marchant, 1998; Forde, 2002). Forde (2002) found an indirect relationship between fear-related and aggression-related behaviour. Sows who showed 'bold' behaviour when confronted with an unfamiliar person were more likely to show aggressive behaviour towards the stockperson.

Aggression towards piglets

A more extreme form of behaviour that affects piglet mortality is aggressive behaviour from females towards their own offspring. In pigs, this problem is more common in gilts than in multiparous sows (van der Steen *et al.*, 1988; Cronin and van Amerongen, 1991). Knap and Merks (1986) studied piglet-directed aggressiveness in two purebred and one crossbred populations of sows and found that 7-13 % of the sows showed aggressive behaviour that led to wounding or death of the piglets. Similar results are reported by van der Steen *et al.* (1988).

This type of behaviour is possibly caused by the gilt being kept in a barren environment. Because of lack of experience, the piglets are regarded to be unknown objects and perceived as a potential danger, triggering the aggressive behaviour (Knap and Merks, 1986). Aggression towards offspring can also be related to fear. In a recent study, Forde (2002) measured fear response of sows when confronted with an unknown human. Sows showing high levels of fear were also more likely to savage their piglets.

Aggressive behaviour towards piglets is partly genetically controlled. Daughters of aggressive sows show twice the incidence of aggressive behaviour, compared to daughters of non-aggressive sows (van der Steen *et al.*, 1988). Heritability estimates for sow aggressiveness towards piglets ranges from 0.12 to 0.9 (Knap and Merks, 1986; van der Steen *et al.*, 1988).

Some factors affecting pre-weaning growth

Nursing behaviour

The sow does not have teat cisterns, and milk is only available to the piglets for very short periods at a time, during milk letdown (Algers, 1993). Therefore, it is very important that the piglets are synchronized at the udder during a nursing. A teat order is settled during the first days and stays fairly constant until weaning. The establishment of a teat order limits the amount of competition and fighting among piglets at the udder (Algers, 1993).

During the first phase of a nursing bout, the piglets assemble at the udder and find their teat. The assembling may be initiated by the sow grunting, or spontaneously by the piglets themselves. External stimuli may also trigger sow or piglets to initiate a nursing, such as the sound of other litters suckling. Some sows have been seen to nurse while standing, but normally sows lie on their side so that both rows of teats are available to the piglets (Fraser, 1980). Inability to expose all teats during nursing is more common in older sows than in gilts, and may seriously limit growth rate and chances of survival of the piglets (English and Smith, 1975).

When the piglets have arranged themselves at the udder, they start massaging their teat. This massaging lasts for about a minute, and is necessary to stimulate milk ejection. During this phase, the sow grunts rhythmically. After a minute or so, the sow increases the rate of grunting, and the piglets stop massaging and start sucking on their teat. Milk letdown occurs about 20 seconds following the peak in grunt frequency. Milk letdown lasts for approximately 10-20 seconds, and afterwards the piglets resume massaging their teat. The nursing is terminated by the piglets leaving the udder, falling asleep at the udder, or by the sow sitting or standing (Fraser, 1980).

During the first 24 hours after farrowing, the number of nursings stabilises at about one per hour (Algers 1993). Nursings occur more seldom as the piglets grow older, and with time the number of nursings that the sow initiates decreases and the number of nursings that the sow terminates increases. A recent study by Valros *et al.* (2002) shows behavioural changes indicating an ongoing weaning process in the sow, starting already in the first week of lactation.

Valros *et al.* (2002) also showed that sow's have individual nursing patterns that are repeatable within sow and lactation. These results indicate that there may be genetic differences in nursing behaviour. Furthermore, the frequency of successful nursings (nursings resulting in milk letdown) was positively related to piglet growth. However, the variation in nursing frequency between sows was small, indicating that there may be limited possibilities for improvement.

Milk production and piglet growth

Milk production during early lactation can vary widely between sows. An inadequate production of milk can have several causes, such as various disease conditions or hormonal abnormalities, as well as environmental factors (Fraser, 1990). Disturbance of the communication between sow and piglets decreases the synchronisation within the litter at nursing and decreases the amount of milk the sow produces (Algers and Jensen, 1985, 1991).

Mackenzie and Revell (1998) show in a comparison of data from the literature that milk yield has clearly increased in the last 20-30 years. This improvement can be attributed to both genetic and environmental factors. Since there has not been a direct selection on milk production in sows, a genetic progress has to originate from selection criteria that are indirectly related to milk yield. Mackenzie and Revell (1998) suggest that possibly correlated traits are growth rate and litter size.

It is very difficult to obtain direct measurements of sow milk production, because teat stimulation and oxytocin release is necessary for milk ejection. Indirect measures are instead often used; for example the weigh-suckle-weigh method when litter weight is measured directly before and after each suckling. This method is not practical to use on a larger scale, where milk production instead has to be estimated from piglet growth rate from birth to start of creep feeding. Generally, milk production of the sow (in grams per day) can be approximated by multiplying litter weight gain (grams per day) by 4 (Whittemore and Morgan, 1990). The accuracy of the method differs between reported estimates (Etienne *et al.*, 1998).

The newborn piglet has very limited body fat reserves, and early growth is mainly focused on deposition of body fat. Growth rate during the first weeks after birth is highly variable between litters. Thompson and Fraser (1988) showed that weight gain during the first couple of days after birth was not determined by birth weight but later in lactation, rate of gain became more related to body weight. Piglets that were heavier at 10 days of age, gained more weight from then on than piglets that were not as heavy at 10 days of age (Thompson and Fraser, 1988). This could be related to nursing behaviour of the piglet. Algers and Jensen (1991) showed that the intensity and duration with which a piglet stimulates a teat during massage after a nursing affects milk production of that specific teat. It is possible that heavier piglets are able to provide more effective massage. If massaging of the udder following milk letdown is prevented, average daily litter weight-gain was shown to decrease (Algers and Jensen, 1991).

Maternal behaviour in sows – a Nordic project

To deal with the problem of high piglet mortality and increasing importance of good maternal ability in sows, a Nordic network was started in 1998. Within the network a co-operation project was performed, involving scientists in the fields of genetics, ethology and veterinary medicine. The purpose of the project was to combine research areas focusing on sow behaviour, physiology and genetics to gain knowledge that may be used to improve piglet survival and growth. A large number of characteristics involved in maternal ability in sows was studied, among them nest building, farrowing duration, activity during lactation, carefulness and sows' reaction to a screaming piglet, physiological regulation during lactation, milk production, nursing motivation and nursing behaviour, and aggressiveness towards piglets and humans (Rydhmer, 2002). The studies in this thesis were performed as part of this Nordic project.

Aim of study

The purpose of this thesis was to gain knowledge about the genetic background of different aspects of maternal ability in sows, and to investigate how to introduce maternal ability into the breeding goal to improve early piglet performance. In this thesis, piglet mortality, early growth, birth weight and different sow behaviour traits are used as measures of maternal ability.

The specific aims were:

- to investigate the genetic background of different causes of death in piglets and their relation to piglet birth weight,
- to investigate the possibilities to use measures of sow behaviour as an indication of maternal success and as possible selection traits for improved piglet survival rate,
- to analyse how selection for improved piglet survival and growth may affect sow body condition during lactation, and
- to analyse the genetic relationships between piglet survival and piglet growth.

Overview of investigations

Material and methods

Data collected at the herd at Funbo-Lövsta research station (Swedish University of Agricultural Sciences) between the years of 1983 to 2000, were used for publications I-III. All sows were purebred from the Swedish Yorkshire breed. Herd size was around 100 sows. Publication II includes data also from crossbred litters, whereas publications I and III only includes records from purebred litters. Publication I includes records on first parity sows only, whereas publications II and III include records from all parities. All sows were kept loose in farrowing pens (Figure 2) during lactation.

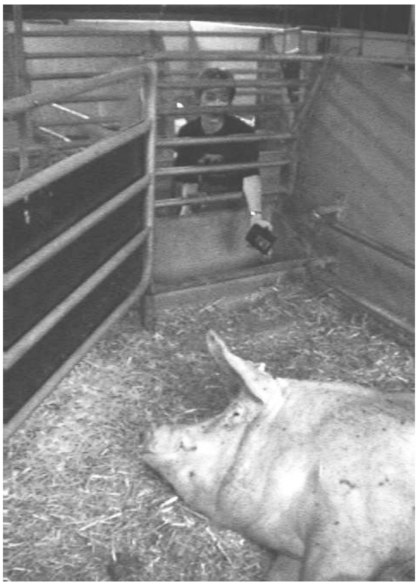
Figure 2. Sows in Sweden are kept loose in farrowing pens during lactation.

During six years, between 1983 and 1989, this herd was used in a selection experiment. Animals were then selected for lean tissue growth rate in two lines, one on low dietary protein content and the other on high dietary protein content. After the animals reached a body weight of 90 kg they were given the same feed and norm. After 1989, the herd has been used in various research projects, including projects on nutrition, genetics, and animal husbandry but not selected for any specific traits.

Piglets were weighed individually within 24 hours after birth, at three weeks of age, at weaning and at nine weeks of age. Until 1992, piglets were weaned at six weeks of age; after 1992, piglets have been weaned at five weeks of age. These are the weaning ages normally applied in Swedish herds. Dead piglets were also weighed, and the stable staff determined the cause of death. The sow was weighed at farrowing and at weaning, and at the same time backfat was measured by ultrasonic measurement. During lactation, the sow was fed according to litter size.

Publication II includes data from nine Swedish Yorkshire breeding herds, in addition to the data collected at the research station. The breeding herds produce purebred animals, to be used as sires and dams, and some breeding herds also produce crossbred gilts. Half of the litters produced in the breeding herds included in this study were cross-bred, sired with Swedish Landrace. Herd size ranged from about 20 to 300 sows. The breeders take part in a common breeding programme with the following goal: high daily gain, high leanness, high feed efficiency, large litters, short farrowing intervals and strong legs. Daily gain from birth to 100 kg and backfat thickness at 100 kg are recorded in the breeding herds. Litter size (number of piglets born alive) and farrowing interval are recorded in the breeding herds and in the multiplier herds. Growth rate from 35 to 104 kg, lean percentage in the carcass, feed conversion ratio, leg conformation score and osteochodrosis score are recorded at a test station.

The behaviour traits recorded in publication II were: sow's reaction to a piglet scream, sow's reaction to her piglets being handled, and avoidance of and aggression towards the stockperson. All recordings of behaviour data were performed by the stockperson.



The piglet scream test was used to test a sow's reaction to the distress call from a piglet, as when it is being crushed under the sow (Thodberg, *et al.*, 1998). The test was done on the farrowing day or the following day. When the sow was lying on her side, but not nursing, the stockperson quietly placed a small tape recorder into the pen and the recorded sound of a screaming piglet was played to the sow for approximately 20 seconds (Figure 3). The same scream recording used on all the farms, was recorded from a piglet that was held and squeezed firmly by a person.

Figure 3. Illustration of the piglet scream test

The sow's maximum response to the sound was scored into four ordered categories: no reaction, lying down and looking for the sound, sitting up, or standing up.

The piglet handling test was performed around day 4, in connection with routine treatment of the piglets, such as castration and iron supplementation. If no piglets were castrated in a litter and no iron was given, the stockperson was instructed to pick up the piglets anyway, hold them and, if necessary, squeeze them lightly until they screamed. The sow's body posture at the start of the test, just before the piglets were picked up by the stockperson, was recorded in four ordered categories: 1) lying on her side, 2) lying on her belly, 3) sitting, or 4) standing. After the piglets were taken out and handled, the sow's maximum response to the handling of her piglets was recorded using the same four categories. The response to the piglets being removed from the pen and subjected to handling was then analysed as the difference in category number between sow posture after and before the test.

Avoidance of the stockperson was used as an indicator of fear and was measured in connection with the piglet handling test by recording how the sow positioned herself in relation to the person handling the litter (Figure 4). Sows that moved toward the handler were given a score of 1, sows that did not move at all were given a score of 2 and sows that moved away from the handler were given a score of 3. Sows that did not stand up were regarded as not having moved, and were scored 2. Aggression towards the stockperson was recorded at the same time. Sows perceived as aggressive by stockpeople were scored 1, whereas non-aggressive sows were given a score of 0.

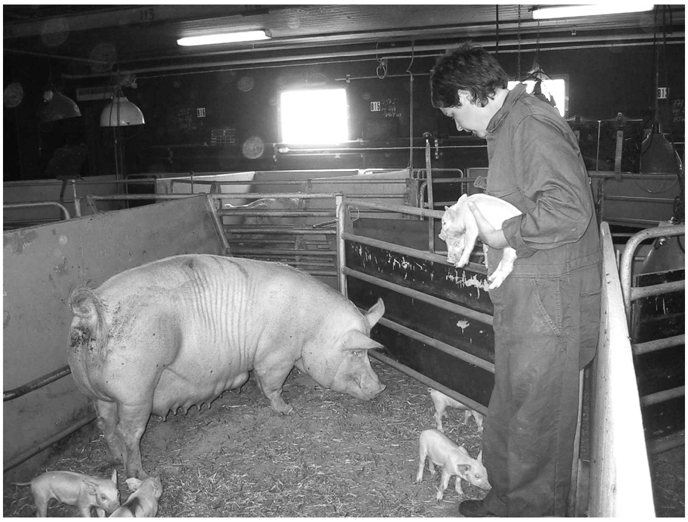


Figure 4. Fear of humans was measured as avoidance of the stockperson during piglet handling.

Together with information on sows' responses in the behaviour tests, the breeding herds also reported the number of piglets that had died during the first four days after birth.

Statistical methods

In publications I and III, the software package DMU (Madsen and Jensen, 2000) was used for parameter estimation. (Co)variance components were estimated using the average information (AI) residual maximum likelihood (REML) algorithm (Jensen *et al.*, 1997).

Publications I and II also include parameters estimated using a threshold-linear model. In these models, the threshold concept was applied for the categorical variable, assuming an underlying non-observable variable called liability. If the liability exceeds a certain threshold, the observable variable falls into the next category. The model was formulated in a Bayesian context, in which the data vector was augmented with the unobservable liabilities. (Co)variance components were estimated using the Gibbs sampling algorithm, implemented in Korsgaard *et al.* (1999).

Animal models were used for all traits. Direct and maternal effects were included in the linear models for piglet birth weight and growth rate, and in publication III also for mortality of liveborn piglets. Due to computational reasons, the threshold-linear models included only the genetic effect of the sow.

Comments on data and genetic analyses

For the genetic analyses of piglet traits (survival, birth weight, growth), our intention was to use a full model including the direct genetic effect of the piglet, the maternal genetic effect of the sow, a random permanent environmental effect of the sow and a random litter effect. However, this model was not possible to use because of convergence problems. Separation of genetic maternal effects from systematic environmental effects of the sow and litter effects requires a good data structure, with repeated observations on each sow (Meyer, 1992). During the selection experiment at the Funbo-Lövsta research station, half of the selected sows were culled after their first lactation and the other half after their second litter. This has contributed to a skewed age structure in the data where over 40 percent of the sows included only have records from one litter. In publication I, this problem has been handled by only analysing data from first parity litters. In publication III, records from all parities are included, but the permanent environmental effect had to be excluded from the model because of computational problems in bivariate analyses.

In publications I and II, a threshold model was used for analysing categorical data. Because of limitations in the program at the time of the analyses, only one genetic effect could be included in the models. The models for piglet birth weight and mortality had to be simplified to include only the genetic effect of the sow and not the direct effect of the piglet. This is probably a more serious simplification with regard to birth weight than it is for piglet mortality where the direct effect seems to be very low.

Large differences in sow behaviour were seen between the experimental herd and field data (publication II). The sows at the experimental herd are individually handled by the stockperson much more often than sows in breeding herds, and they showed lower levels of fear and aggression towards the stockperson, compared to sows in the breeding herds. Overall, sow behaviour differed significantly between farms, and it is possible that this is related to different ways of performing the tests or other environmental factors we could not control. Farms are genetically connected through the use of AI. However, quite a large proportion of the boars used in our data only sired one litter, or were only used on one farm.

The behaviour records and the information on early mortality from the breeding herds (publication II) are not available from the litter recording scheme. These data were collected only for the purpose of this study. Consequently, the data set is small, information is only available from a little over 1000 litters. This obviously makes the precision of the estimates of genetic parameters low.

Results

The presentation of the results given here, and the following discussion, will focus on the genetic parameters, mainly the genetic correlations between traits. Heritabilities for most traits were low, and influenced to a great extent by environmental factors. The effect of environmental factors are commented more upon in each respective publication.

Heritabilities for piglet mortality, birth weight and growth (publications I-III)

In publications I-III, genetic parameters for different definitions of piglet mortality were estimated. Heritabilities (maternal, or when regarded as a trait of the sow only) were low for all mortality traits, ranging from 0.01 to 0.04 in a linear model and from 0.05 to 0.15 in a threshold model. The highest heritability was estimated for stillbirth, when only including records from first parity sows (publication I). In a preliminary analysis for total mortality, including stillborn piglets, the direct heritability was estimated at less than 0.0005 (publication I). When analysing pre-weaning mortality of liveborn piglets and looking at records from all parities, the direct heritability was substantially higher, 0.01 (publication III).

The maternal genetic component had a larger influence on birth weight, compared to the genes of the piglet. The maternal heritability was estimated at 0.15-0.19 and the direct heritability at 0.04-0.07 (publications I and III). Direct and maternal heritabilities for pre-weaning growth were in the same range, 0.13 and 0.16 respectively. For post-weaning growth until 9 weeks of age, the direct effect accounted for a larger part of the total variation compared to the maternal effect. The direct and maternal heritabilities were estimated at 0.20 and 0.06, respectively (publication III).

Genetic relations between piglet mortality, birth weight and early piglet growth (publications I, III)

The genetic correlations are summarised in Table 1. In publication I, we found positive genetic correlations between on one hand direct and maternal effect for piglet birth weight, and total mortality and stillbirth on the other, whereas negative correlations were found between crushing and both direct and maternal effect for birth weight. In publication III, we found a negative correlation between the maternal effect for mortality of liveborn piglets and the maternal effect for birth weight. We also found a significant positive correlation between the direct effect for birth weight and the maternal effect for stillbirth, indicating that piglets with genetic capacity for a high birth weight have more stillborn piglets when they become mothers.

Study III shows a positive correlation between the maternal effect for piglet birth weight and the maternal effect for growth rate from birth to weaning and growth rate from weaning to 9 weeks of age. However, we also estimated a significantly negative correlation between the direct effect for birth weight and the direct effect for growth rate from birth to weaning. Fairly low correlations were found between growth from birth to weaning and growth from weaning to 9 weeks of age (0.03-0.40).

We found no significant correlations between the maternal effect for growth rate during lactation and the maternal effects for stillbirth or mortality of liveborn piglets. We found negative direct-maternal correlations between mortality of liveborn piglets and pre-weaning growth, but a positive, although not significant, correlation between the direct effect for mortality of liveborn piglets and the direct effect for growth rate during lactation (publication III).

Direct-maternal genetic correlations within traits were negative for mortality of liveborn piglets, growth from birth to weaning, and growth from weaning to nine weeks of age. Direct-maternal correlation for birth weight was estimated at zero (publication III).

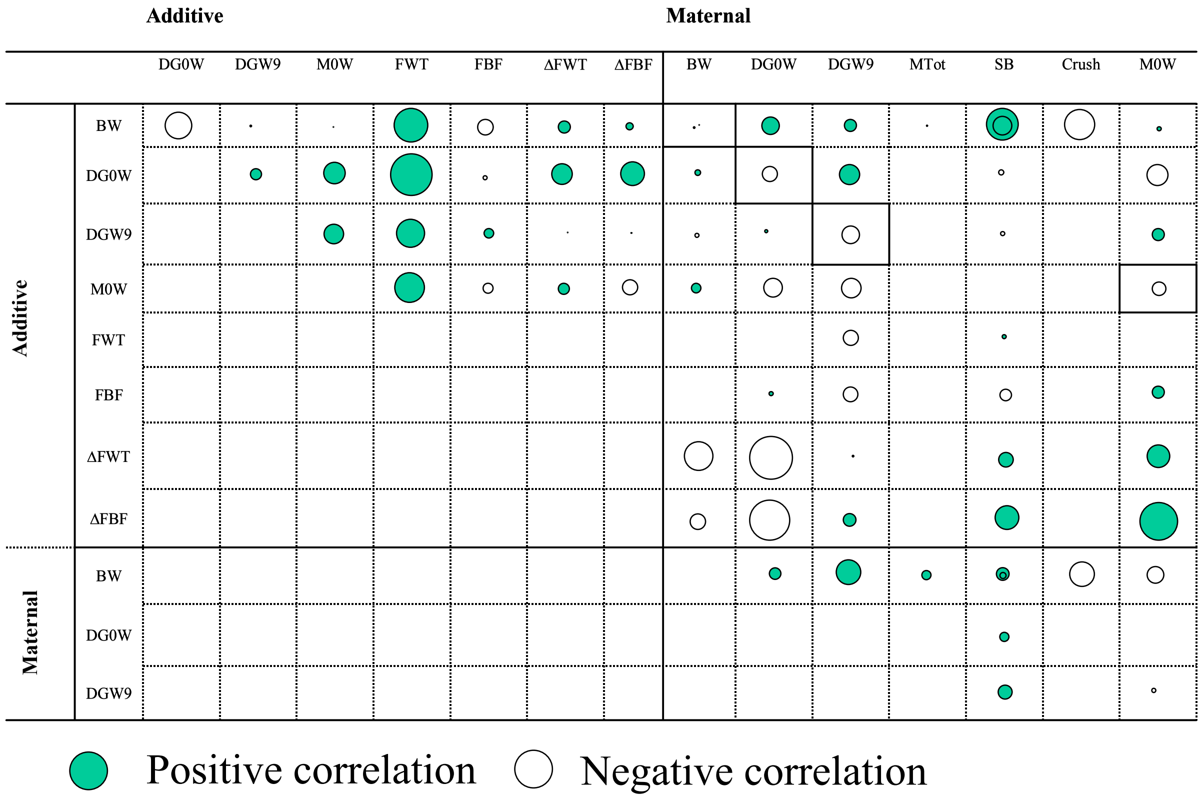
Genetic relations between sow behaviour traits and piglet mortality (publication II)

In publication II, we studied the genetic background to different sow behaviour traits and their relation to piglet mortality. All behaviour traits had low heritabilities, ranging from 0.01 to 0.08. We found indications of a negative genetic correlation between a sow's response in the piglet scream test and piglet mortality, indicating that a strong response in the scream test is genetically associated with improved survival. Furthermore, we found indications of a positive correlation between sow's avoidance of the stockperson during piglet handling and piglet mortality, indicating that a high level of fear is genetically associated with a high mortality rate. We could not see any relation between sow's aggression towards the stockperson and piglet mortality.

Genetic relations between sow body condition and piglet mortality and growth (publication III)

The genetic correlations are summarised in Table 1. In publication III, we studied the genetic background to sow weight and backfat at farrowing and loss of weight and backfat during lactation, and their relation to piglet mortality and growth. Estimated heritabilities for the different measures of sow body condition were low to moderate, ranging from 0.10 to 0.47. We found strong negative genetic correlations between loss of weight and backfat during lactation and the maternal effect for piglet growth during lactation, indicating that a large loss of weight and fat reserves is associated with a high piglet growth rate. The corresponding correlations to the maternal effect for mortality of liveborn piglets were positive, indicating that a large loss of weight and backfat is associated with a higher survival rate.

Table 1. Summary of estimated genetic correlations. A circle, where the diameter is proportional to the size of the correlation, represents each correlation. Filled circles represent positive correlations and open circles represent negative correlations. A solid frame indicates direct-maternal correlations within trait



List of abbreviations
BW: birth weight
DG0W: daily gain from birth to weaning
DGW9: daily gain from weaning to 9 weeks
MTot: Total mortality
SB: Stillbirth
Crush: Mortality due to crushing
M0W: Mortality from birth to weaning (of born alive)
FWT: Farrowing weight
FBF: Farrowing backfat
ΔFWT: Loss in farrowing weight
ΔFBF: Loss in farrowing backfat

General discussion

The selection goal should include a measure of maternal ability in addition to litter size. In the research this thesis is based on, we have investigated the genetic background of a number of traits related to maternal ability of sows, and we have estimated genetic correlations between these traits and piglet survival and growth. Our results show that there is genetic variation in most traits studied, although with a low heritability. A direct and a maternal component can be identified for pre-weaning mortality, piglet birth weight and growth, and negative direct maternal correlations were estimated for pre-weaning mortality and growth.

There are different ways to go about using various sources of information in a breeding programme to improve early piglet performance. Selection could be based on the goal traits themselves, piglet survival and piglet growth. Selection could also be based on correlated traits that have a higher heritability or that are easier to record. Records can be handled on a sow level or on a piglet level. An advantage of handling records on a sow level is that there is no need to keep track of records from individual piglets. However, the existence of negative genetic direct-maternal correlations, shown in this study and other studies (*e.g.* Van Arendonk *et al.*, 1996; Lund *et al.*, 2001), indicate that ignoring the direct effect may have negative effects on the piglets' viability and growth. This will lead to a decreased efficiency of the selection, and realised genetic progress will be less than expected.

In the following, I will discuss possibilities to select for improved survival and growth, based on the genetic parameters estimated in publications I-III.

Selection directly on improved piglet survival and growth

Piglet mortality

Heritabilities for mortality estimated in this study were low, and in the same range as previous results (Rothschild and Bidanel, 1998). A higher heritability was estimated for stillbirth (0.15 in a threshold model), compared with total mortality or crushing (0.05 and 0.06 respectively in threshold models). However, these heritabilities are not much lower than the heritability for litter size, for which selection has proven successful (*e.g.* Johnson, 1999).

In publication I, we excluded the direct effect for all mortality traits. This was based on a preliminary analysis of total mortality where we found a direct genetic heritability of less than 0.0005. However, in publication III, we found a higher direct heritability when analysing mortality of live born piglets, and we estimated a negative genetic correlation between the direct and the maternal effect. A negative direct-maternal genetic correlation was also found by Van Arendonk *et al.* (1996) and Lund *et al.* (2001). Lund *et al.* (2001) found breed differences in the influence of the genetic effects on mortality. A larger heritabilities, both direct and maternal, were found for pre-weaning mortality of live born piglets in the Landrace breed compared to the Yorkshire breed.

Pre-natal and post-natal mortality seem to be controlled by different genes, and these traits should be treated separately in a breeding programme. Our results indicate that it would be sufficient to regard prenatal mortality as a trait of the sow only. The sow's genes also influence mortality of live born piglets to a higher degree than the piglet's own genes. The direct effect may have to be included as well, as there seems to be a negative genetic direct-maternal correlation for postnatal mortality (publication III; Van Arendonk, 1996; Lund *et al.*, 2001).

Crushing is one of the most common causes of postnatal mortality (*e.g.* Glastonbury, 1977). In publications I and II, we defined crushing as a specific trait, and in publications II and III, we analysed total mortality of liveborn piglets. The more specific definition of the trait in publication I did not yield a higher estimated heritability (comparing results from linear analyses in publication I and III and results from threshold models in publication II). In our data, experienced staff determined cause of death, but it is very difficult to determine the true cause of death of a piglet only by visually inspecting the dead piglet. Therefore, total mortality of live born piglets is easier to record, and our results indicate no reason for trying to make a more detailed specification of cause of postnatal death in breeding programmes.

Early piglet growth

It is not only important to have piglets that survive until weaning, it is also important that they maintain a good growth rate. A recent study by Solanes *et al.* (2003), using the same data set used in this study, showed favourable genetic correlations between piglet weights at weaning and growth rate during the fattening period. These results indicate that selection for improved piglet growth during lactation will have positive effects on later performance of the slaughter pig.

Piglet growth from birth to weaning is affected by both maternal genetic effects and the piglet's own genes. According to our results, the maternal heritability was slightly higher than the direct, 0.16 and 0.13 respectively (publication III). Piglet growth after weaning is mainly controlled by the piglet's own genetic capacity for growth. The decreasing influence of maternal effects with age has also been reported by Kaufmann *et al.* (2000) and Hermesch *et al.* (2001). The direct heritability for daily gain from weaning to nine weeks of age was estimated at 0.20, compared with a maternal heritability of 0.06. Genetic correlations between the two growth periods were positive or close to zero. The rather low correlations may be caused by the fact that the weaning process is very stressful for the piglets, and it is usually followed by a period of depressed growth and even impaired health for the piglets.

Our results show significant negative genetic direct-maternal correlations for daily gain both from birth to weaning and from weaning to nine weeks. Negative genetic direct-maternal correlations have also been estimated for growth during performance testing (Bryner *et al.*, 1992). This indicates that a selection programme aimed at improving early piglet growth, should focus both on the sow trait and on the piglet trait. In practice, this means that weights of each individual piglet have to be recorded. Obviously, this is more labour demanding than weighing the whole litter. On the other hand, a selection strategy that focuses only on the sow may lead to a deterioration of the piglet's own capacity for growth, and the realised genetic progress in early growth will be less than expected.

Relation between growth and mortality

Previous results based on partly the same data used in this study, reported a high and favourable genetic correlation between total piglet mortality and piglet growth from birth to three weeks. Only the genetic effect of the sow was considered, and the results indicated that selection of sows with genes for a high piglet growth rate will lead to a correlated response in improved survival rate (Högberg and Rydhmer, 2000). Using a similar model, Huby *et al.* (2003) found a moderate favourable genetic correlation between mean piglet weight at weaning and pre-weaning survival rate. However, Huby *et al.* (2003) also found an unfavourable genetic correlation between mean weaning weight and stillbirth rate.

In our study, we included the direct genetic contribution of the piglets on growth and mortality. We also analysed prenatal mortality separate from postnatal mortality. Our results do not show the same clear favourable association between survival and growth rate as in the previous study by Högberg and Rydhmer (2000). Correlations between stillbirth and direct and maternal effects for daily gain from birth to weaning were low and not significant. The maternal-maternal correlation between daily gain from birth to weaning and mortality of liveborn was estimated at zero. The maternal genes that influence early growth seem to be different from the maternal genes that influence postnatal mortality. We found an unfavourable correlation between the direct effect of growth from birth to weaning and the direct effect for postnatal survival. This indicates that selection of pigs with a genetic capacity for a high growth rate may have a negative effect on piglet viability. Similar results were found by Knol *et al.* (2001a).

It is difficult to estimate the relation between survival and growth because of the lack of information. Obviously, dead piglets do not have records on later growth rates. None of the genetic correlations between growth rate and survival were significantly different from zero. Nevertheless, our results indicate that a breeding programme designed to improve both piglet survival and early growth should include both these traits as selection traits, because there is no clear evidence that they are favourably correlated to each other.

Selection on birth weight to improve survival and growth

There is a favourable phenotypic relationship between a high piglet birth weight and survival. Litters with low mean birth weights generally have a higher mortality rate (Fraser, 1990), and piglets that die during lactation have a significantly lower birth weight compared to their surviving litter-mates (*e.g.* Dyck and Swierstra, 1987). Roehe and Kalm (2000) showed that the single most important risk factor that affects pre-weaning mortality is the piglet's individual birth weight.

Slightly higher heritabilities have been reported for birth weight than what has been found for mortality. Roehe (1999) reported a direct heritability of 0.08 and a maternal heritability of 0.22. In this study, we estimated somewhat lower heritabilities for first parity sows, 0.04 and 0.15 for direct and maternal heritability respectively (publication I). The estimates from data including all parities were similar to those reported by Roehe (1999): 0.07 and 0.19 for direct and maternal heritability respectively. The higher heritabilities for birth weight compared with piglet mortality indicate that birth weight could be a possible selection trait to improve piglet survival (Roehe and Kalm, 2000).

We estimated genetic correlations between birth weight and different definitions of piglet mortality in publications I and III. The results from both papers point in the same direction: selection for an increased piglet birth weight can possibly lead to a correlated response in improved survival of live-born piglets, but at the same time such selection can be expected to increase the incidence of stillborn piglets. The suggested favourable relationship between birth weight and survival does seem less obvious when considering selection experiments where selection for lean growth has resulted in a correlated increase in piglet birth weights. Although the selected lines had a higher birth weight, they also had a higher incidence of stillborn piglets (Vangen, 1972; Kerr & Cameron, 1995) and a higher mortality from birth to weaning (Vangen, 1972).

Mersmann *et al.* (1984) found that piglets born from genetically leaner sows seem more physiologically immature at birth. Results from Herpin *et al.* (1993) agree with these findings. Herpin *et al.* (1993) showed that in a line selected for lean growth piglets were born heavier but with lower percentages of carcass protein, fat and mobilisable fat. Knol (2001b) compared different selection strategies to improve piglet survival and growth, based on the piglet's own genetic capacity for these traits. He showed that selection for increased birth weight did not result in a correlated improved survival rate. Correspondingly, litters with high breeding values for survival did not have a higher birth weight. A physiological study of piglets with high breeding values for survival showed that these piglets had proportionally larger inner organs such as liver, small intestine, and stomach. They also had a higher liver and muscle glycogen concentrations, higher total amount of liver glycogen, and a higher body fat percentage, compared with piglets with poor breeding values for survival (Leenhouwers *et al.*, 2002).

In publication III, we estimated genetic correlations between birth weight and early piglet growth. Positive maternal-maternal correlations between birth weight and growth rate before and after weaning indicate that sows with genetic capacity to give birth to piglets with a high birth weight also have a higher growth rate in their litters between birth and nine weeks of age. However, we estimated a strong negative direct-direct correlation between birth weight and daily gain from birth to weaning. Piglets with genetic capacity for a high birth weight have a poorer genetic capacity for growth during lactation.

It seems as if survival is more related to body composition and maturity of the piglet than to birth weight as such. Genetic selection for higher birth weight is not a recommendable strategy to improve survival or piglet growth during lactation. An alternative to selection for increased birth weight is to focus on uniformity in birth weight within litters. Several studies have shown that uniformity in birth weight is favourably correlated to survival rate on the phenotypic scale (English and Smith, 1975; Roehe and Kalm, 2000).

Heritabilities ranging from 0.08 to 0.11 have been estimated for within-litter variation in birth weight (Högberg and Rydhmer, 2000; Hermesch, 2001; Damgaard *et al.*, 2003; Huby *et al.*, 2003). Damgaard *et al.* (2003) found that uniformity in birth weight was strongly genetically correlated to uniformity in weight at weaning. Estimated correlations suggest that selection for uniformity in birth weight may improve piglet survival (Damgaard *et al.*, 2003; Huby *et al.*, 2003). These results are supported by Knol *et al.* (2001b) who predicted that selection for the piglet's own ability to survive will lead to more uniform litters. Furthermore, Damgaard *et al.* (2003) predicted that selection for uniform litters will have positive effects on piglet growth rate.

Selection on sow behaviour to improve survival

Sow behaviour during lactation has a large influence on the piglets' chances of survival. If behaviour is to be included in a breeding programme, the trait has to be defined so that large-scale recording is possible – a rather challenging task. The conditions under which recordings are performed must be strictly standardised to reduce environmental variation and increase heritability of the traits. The behaviour or test used to measure the behaviour needs to be very simple. However, simplifications should not be so drastic that the biological importance of the recorded traits is lost.

In this study, we chose to record the sow's behavioural response to a test situation (the screaming piglet test) and her behavioural response to a situation that is part of normal farm routine (the piglet handling test). Our aim was to connect the recordings to normal farm routines, to make it as convenient as possible for the farmers to perform the recordings. The piglet scream test was performed in connection to the first handling of the litters, the first day after farrowing, and the piglet handling test was performed around day 4 when litters are handled for castration and are given iron supplements.

The sow's response to piglet handling on day 4 showed very little genetic variation and a heritability of 0.01. The other three behaviour traits measured were sow's response to a screaming piglet, fear of stockperson, and aggression towards stockperson. All three traits had heritabilities in the same range as those for mortality. Hemsworth *et al.* (1990) estimated a substantially higher heritability at 0.38 for fear of humans in gilts. This higher heritability could partly be explained by the more standardised test used in Hemsworth's study, compared to ours.

Contrary to the studies by Wechsler and Hegglin (1997) on the piglet scream test and by Hemsworth *et al.* (1999) on fear of humans, we found no phenotypic relationship between either of these traits and piglet survival. However, the genetic correlations between the traits found in our study indicate that selection of sows with a strong response in the screaming piglet test can be expected to give a correlated response in improved piglet survival. Selection against sows that avoid the stockperson during piglet handling can also be expected to lead to an improved piglet survival rate. The relation between aggression towards a stockperson and piglet survival is not clear from our result: we estimated the genetic correlation at zero but with a very large posterior standard distribution.

Of the behaviour traits studied, response in the piglet scream test and fear of the stockperson during piglet handling seem to be related to piglet survival and thus could possibly be used as selection traits. However, the heritabilities for both traits were low and not much higher compared to survival itself. The piglet scream test is not easier to record and it cannot be recorded earlier than survival. The fear test, however, has the advantage that it does not have to be recorded during lactation as was done in this study. Fear can be observed in young animals, giving the information early in life, and in both sexes, which is an advantage in breeding evaluation. Janczak *et al.* (2002) recorded fear of humans in young gilts and found that gilts showing low levels of fear had improved maternal behaviour and lower mortality in their litters when they later became mothers. However, more research is needed to investigate the genetic relation between fear responses at different ages and in different stages in life. A study by Wallenbäck (2002) showed that fear of humans measured in gilts around the time of sexual maturation showed very little phenotypic relation with later fear responses during lactation and reproductive success.

A recent study by Forde (2002) showed that a high level of fear in gilts, displayed by "shy" behaviour when confronted with a human, were more likely to savage their piglets. Gilts who showed "bold" behaviour with an unfamiliar human were more likely to be aggressive toward the stockperson. If these phenotypic relationships reflect an underlying genetic correlation, selection against fear of humans in sows could lead to a higher level of aggression towards the stockperson. However, low levels of fear would be beneficial for the piglets, and for the sow from a welfare point of view since fear is closely related to stress. Because of computational problems, it was not possible for us to estimate the genetic relationship between fear of humans and aggression towards humans.

An alternative way of measuring behaviour was presented by Vangen *et al.* (2002), who used a questionnaire in breeding herds in Norway that allowed the farmers to judge the behaviour of their sows. Farmers answered questions about, for example, the sow's carelessness around her piglets early in lactation, reaction to piglets being handled, and fear and aggression during routine management. The heritabilities estimated by Vangen *et al.* (2002) were considerably higher than those we found for fear during management (0.29 vs. 0.08), aggression during management (0.19 vs. 0.08) and reaction to piglet handling (0.25 vs. 0.01). These comparably high heritabilities are very encouraging, and it appears that by letting the farmers judge behaviour over a longer period of time, instead of making a single test, the environmental variation can be reduced, and a truer estimate of the sow's temperament can be made. However, the studied herds were rather small, and it can be assumed that the farmers know their individual animals quite well. It remains to be seen if the heritabilities are equally high on larger farms, where farmers may have less knowledge about the behaviour of individual animals.

Consequences of selection for improved maternal ability for sow body condition

Strong genetic selection for lean meat production efficiency has markedly changed body composition in both the slaughter pig and the reproducing sows during the last 30 years (de Vries and Kanis, 1994; Edwards, 1998). Milk production requires a great deal of energy. The sow usually cannot meet requirements by increased food intake and will use body reserves of fat and protein to maintain milk energy output. Large losses of body weight are detrimental for later reproduction. First parity sows who use up large amounts of body reserves during lactation have impaired ability to re-breed, reduced subsequent litter sizes and reduced milk production in subsequent litters (Whittemore, 1996).

Loss of body weight during lactation is related to litter size (Rydhmer *et al.*, 1992). Increasing litter size through selection will therefore require that the sows use more of their body reserves to maintain milk production. In publication III, we show that there are also strong genetic correlations between loss of body reserves and maternal effects of piglet survival and growth. If selection is performed on the maternal component for piglet survival or growth during lactation, there will be a correlated genetic change in loss of body reserves. These results agree with phenotypic relationships estimated in a recent study by Valros *et al.* (2003), who showed that a larger weight loss during the third week of lactation seems to be associated with a higher piglet growth rate. Furthermore, sows that turned catabolic early in lactation (high concentration of free fatty acids in the blood) also had a lower mortality rate in their litters (Valros *et al.*, 2003).

Larger losses of body reserves during lactation may lead to an increase in reproductive problems and possibly an increased culling of sows, unless the higher demands for nutrients for milk production are met by an increase in voluntary food intake. A breeding programme to increase piglet survival and growth should therefore pay attention to the sow's body condition and ability to maintain enough body reserves to be able to regain reproductive functions after weaning. Selection for a higher voluntary feed intake during lactation was suggested by Eissen *et al.* (2000).

Conclusions

- Piglet survival can be improved by selection. Pre-natal and post-natal mortality have different genetic background and should be treated separately in breeding programmes.

- A breeding programme to improve piglet survival and early piglet growth need to include both these traits and should include both the direct and the maternal effects for these traits.

- Selection for increased birth weight is not a good strategy to improve piglet survival or growth rate.

- Selecting for sow's response to a screaming piglet or against fear of humans are possible strategies to improve piglet survival, but perhaps not more efficient than selecting on survival itself. Fear, however, has the advantage that it can be measured in the young animal, before it is selected for replacement, and in both sexes.

- A breeding programme to improve piglet survival and growth need to also focus on the sow's ability to remain in good enough body condition to be able to regain reproductive function after weaning.

Future outlook

A high survival rate of the piglets is economically important for the farmer, and highly desirable from an ethical standpoint. There is little doubt that survival should be included in the breeding goal for pigs, together with litter size. The means of doing this, still requires some further investigations.

Improved recordings of survival and growth in the breeding herds increase the possibilities of selection directly on these goal traits. Further studies on the genetic relations between survival and other traits in the breeding goal are needed.

Other traits may also be valid for consideration in the breeding programme. Fear of humans is relatively simple to record and can be recorded at a young age and in both sexes. Lower levels of fear would also increase sow welfare, together with piglet welfare (improved piglet survival). Further research is needed to investigate the genetic relationship between fear measured in the young animal and later reproductive performance.

Genetic parameters are only valid in the population they were estimated in. The sows in this study were loose-housed in indoor pens. The research behind this thesis, together with other studies within the Nordic project on maternal behaviour, shows that the environment has a large impact on maternal behaviour. However, studies are lacking on genotype-environmental interactions for these traits – it is not known whether the best mother in an indoor production system also is the best sow in extensive systems, such as outdoor production. Existence of genotype-environmental interactions may necessitate different breeding programmes for different production systems.

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