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Genetics of Sow Efficiency in the Finnish Landrace and Large White Populations

Doctoral Dissertation

Timo Serenius

Animal Production

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Abstract

The objectives of this study were to determine the selection potential (genetic variation) of sow efficiency traits (prolificacy, longevity), to understand the co-responses (genetic correlations) among sow efficiency traits and other economically important traits (performance, carcass quality, and meat quality), and determine the feasibility of developing breeding value estimates for sow efficiency traits. To meet the objectives, five separate studies were carried out. The prolificacy traits evaluated were total number of piglets born, number of piglets born alive, number of piglets weaned, number of stillborn piglets, percent of stillborn piglets, number of piglets dead during suckling, percent of dead piglets during suckling, gestation length, age at first farrowing, and farrowing interval. The studied longevity traits were lifetime prolificacy (number of piglets per sow's lifetime), length of productive life, and leg conformation (overall leg action, and six symptoms of leg weakness).

The results showed that the sow efficiency traits are generally lowly heritable. The only exceptions are buck kneed on fore legs (conformation trait), age at first farrowing and gestation length, which are moderately heritable. Among leg conformation traits, there was a strong favorable genetic correlation between buck-kneed on the fore legs and overall leg action, whereas no clear genetic association were found between the other leg conformation traits. Moreover, the overall leg action was favorably correlated with length of productive life, indicating that the selection for leg conformation will improve sow longevity through indirect selection. The results showed further that length of productive life and lifetime prolificacy are genetically favorably associated with litter size and farrowing interval.

The most substantial unfavorable correlation among sow efficiency traits exists between litter size and piglet mortality. The current results indicated clearly that the selection only for number of piglets born (totally or alive) will lead to increased piglet mortality. Therefore, the selection should be simultaneously for litter size and piglet mortality.

In general, there was a tendency for sow efficiency traits to be favorably correlated with performance traits, and unfavorably with carcass lean and fat percentages, whereas there was no clear association between sow efficiency and meat quality. Accuracy of estimated breeding values may be improved

by accounting for genetic associations between prolificacy, longevity, carcass, and performance traits in a multiple trait analysis.

Concerning the validity of repeatability model, it appeared that the genetic correlations among litter size between the first and later parity records were lower than the correlations between later parities. All genetic correlations for farrowing interval among different parities were lower than one. These correlations seem to indicate that the litter size from first and later parities, and farrowing interval between all parities should be treated as separate traits in breeding value estimation. In the evaluation of longevity, the estimated heritabilities for length of productive life obtained from linear model analyses were clearly lower than the ones obtained from survival analyses. The higher heritabilities are indicative of the superiority of survival analysis when compared to linear model in the analyses of this type of data.

Based on the results obtained from the current studies, the routine to evaluate genetic ranking based on BLUP-index for leg conformation has been implemented, and the prolificacy index has been updated. Overall leg action score and buck kneed on fore legs are the traits included in the leg conformation index. In the updated prolificacy index, the selection is for total number of piglets born, against number of stillborn piglets and piglet loss during suckling, for lower age at first farrowing and for shorter farrowing interval. For the litter size and piglets survival traits, the first parity results and results from the later parities are treated as different traits. Similarly, only the first two farrowing intervals are evaluated, and they are treated as separate traits. Both the prolificacy and leg conformation traits are analyzed with multiple trait animal model BLUP.

Key words: Genetic correlation, Heritability, Prolificacy, Leg Conformation, Longevity, REML, Survival analysis, Swine

Emakon tehokkuuteen vaikuttavien ominaisuuksien perinnölliset tunnusluvut Suomen sikapopulaatioissa

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Tiivistelmä

Tämän työn tarkoituksena oli selvittää (1) emakon tehokkuuteen vaikuttavien ominaisuuksien (hedelmällisyys, kestävyys) geneettisen vaihtelun suuruus, (2) emakon tehokkuuteen vaikuttavien ominaisuuksien keskinäiset geneettiset yhteydet ja (3) emakon tehokkuuteen vaikuttavien ja muiden taloudellisesti tärkeiden ominaisuuksien (kasvu, rehunhyötysuhde, ruhon laatu, lihan laatu) geneettiset yhteydet. Tarkasteltavia hedelmällisyysominaisuuksia olivat pahnuekoko (yhteensä syntyneiden porsaiden lukumäärä, elävänä syntyneiden porsaiden lukumäärä, vieroitettujen porsaiden lukumäärä), porsaskuolleisuus (kuolleena syntyneiden lukumäärä, porsaskuolleisuus porsimisen ja vieroituksen välillä), ikä ensimmäistä kertaa porsiessa, tiineyden kesto ja porsimaväli. Emakon kestävyyttä kuvaavia ominaisuuksia olivat emakon tuotantoikä, emakon elinikäinen porsastuotos ja jalkojen rakenneominaisuudet (liikuntakyky ja kuusi erilaista jalkojen asentovirhettä).

Tulokset osoittivat, että emakon tehokkuuteen vaikuttavien ominaisuuksien välillä on sekä suotuisia että epäsuotuisia geneettisiä yhteyksiä. Esimerkiksi hedelmällisyys ja jalkojen rakenne (emakon liikuntakyky) ovat geettisesti suotuisasti korreloituneita emakon tuotantoikään. Tämä on edullista, koska emakon tehokkuuteen vaikuttavat ominaisuudet ovat huonosti periytyviä. Tarkasteltavista ominaisuuksista ainoastaan etujalkojen koukkupolvisuus, ikä ensimmäistä kertaa porsiessa ja tiineyden kesto ovat kohtalaisesti periytyviä.

Pahnuekoon jalostuksen kannalta on merkittävää, että porsaskuolleisuuden ja pahnuekoon valillä on positiivinen (epäsuotuisa) geneettinen korrelaatio. Toisin sanoen pelkkää pahnuekokoa jalostettaessa tehdään epäsuoraa valintaa myös porsaskuolleisuuden suhteen. Tämän takia hedelmällisyyden jalostuksessa on huomioitava sekä pahnuekoko että porsaskuolleisuus. Lisäksi tulokset osoittivat, että toistuvuusmallin oletukset eivät täysin toteudu pahnuekoon ja porsimavälin kohdalla, minkä johdosta ensimmäinen pahnuekoko olisi jalostusarvostelussa käsiteltävä eri ominaisuutena kuin myöhemmät pahnuekoot. Vastaavasti kaikki porsimavälit tulisi käsitellä eri ominaisuuksina.

Tulosten perusteella voidaan myös yleisesti todeta, että kasvu ja rehunhyötysuhde olivat suotuisasti ja ruhon laatu epäsuotuisasti korreloitunut emakon tehokkuuteen. Sen sijaan lihan laadun ja emakon tehokkuuden välillä ei selviä korrelaatioita ollut havaittavissa.

Näiden tulosten perusteella rakenneominaisuuksille on kehitetty BLUP-arvostelurutiini ja hedelmällisyysindeksi on uudistettu. Rakenneindeksiin sisällytettyjä ominaisuuksia ovat liikunta ja etujalkojen koukkupolvisuus. Uudistetussa hedelmällisyysindeksissä valittavia ominaisuuksia ovat yhteensä syntyneiden lukumäärä, kuolleena syntyneiden lukumäärä, porsimisen ja vieroituksen välinen porsaskuolleisuus, ikä ensimmäisessä porsimisessa ja porsimaväli. Pahnuekoossa ja porsaskuolleisuudessa ensimmäisen ja myöhempien pahnueiden tulokset käsitellään jalostusarvostelussa erillisinä ominaisuuksina. Vastaavasti porsimavälin kohdalla huomioidaan vain kaksi ensimmäistä porsimaväliä, jotka käsitellään eri ominaisuuksina.

Avainsanat: hedelmällisyys, jalostusarvostelu, kestävyys, korrelaatio, pahnuekoko, periytymisaste, rakenne, sika

List of original articles

The thesis is a summary and discussion of the following articles, which are referred to by their Roman numerals:

I Serenius, T., Sevón-Aimonen, M.-L., Kause, A., Mäntysaari, E.A. and Mäki-Tanila, A. 2004. Selection potential of different prolificacy traits in the Finnish Landrace and Large White populations. Acta Agric. Scand., Sect. A, Animal Sci. 54: 36-43.

II Serenius, T., Sevón-Aimonen, M.-L. and Mäntysaari, E.A. 2003. Effect of service sire and validity of repeatability model in litter size and farrowing interval of Finnish Landrace and Large White populations. Livest. Prod. Sci. 81: 213-222.

III Serenius, T., Sevón-Aimonen, M.-L., Kause, A., Mäntysaari, E.A. and Mäki-Tanila, A. 2004. Genetic associations of prolificacy with performance, carcass, meat quality and leg conformation traits in the Finnish Landrace and Large White pig populations. J. Anim. Sci., in press.

IV Serenius, T., Sevón-Aimonen, M.-L. and Mäntysaari, E.A. 2001. The genetics of leg weakness in Finnish Large White and Landrace populations. Livest. Prod. Sci. 69: 101-111.

V Serenius, T. and Stalder, K.J. 200X. Genetics of length of productive life and lifetime prolificacy in the Finnish Landrace and Large White pig populations. Manuscript, submitted.

Reprints of the original articles I, II, III, and IV are published with the kind permission of the respective copyright owners.

The author participated in planning the studies, carried out the data editing and statistical analyses, and was the main author in all of the five papers.

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1 Introduction

1.1 Sow efficiency

In animal breeding, the objective is to genetically change animals so that high quality (consumer-acceptable) products will be obtained with lower production costs. In piglet production, the extra costs appear when females are anoestrus, when they fail to conceive, and when they fail in raising offspring. Therefore, piglet production cost reductions can be obtained by lowering age at first farrowing and by shortening farrowing intervals. Moreover, a greater opportunity to reduce the costs per piglet may exist by increasing number of piglets weaned. More piglets weaned per sow may be obtained by increasing litter size (total number born), decreasing piglet mortality (both at birth, and between birth and weaning), and by increasing number of litters per sow's lifetime. Here the term 'sow efficiency' is defined as a trait that incorporates all these characters.

In general, the sow efficiency traits described above can be divided into prolificacy (age at first farrowing, farrowing interval, litter size) and longevity (length of productive life or indirectly through leg conformation). However, prolificacy and longevity are highly associated (Yazdi et al., 2000a, 2000b). This association appears, because farmers do not allow sows to remain in the herd that that have poor piglet production or conception problems. Moreover, sows in the fourth and fifth parity produce larger litters when compared to gilts (Clark and Leman, 1986).

Although genetic improvement of sow efficiency appears to be simple, there are several factors that make the selection for these traits challenging. First of all, sow efficiency traits are lowly heritable (Southwood and Kennedy, 1990; Estany and Sorensen, 1995; Roehe and Kennedy, 1995; López-Serrano, et al., 2000; Rydhmer, 2000; Hanenberg, et al., 2001). The only exception is age at first farrowing that has been reported to be moderately heritable (Rydhmer, 2000; Hanenberg et al. 2001). In addition, not all the correlations among the sow efficiency traits are favorable. For example, unfavorable genetic correlations between litter size and piglet mortality have been reported (Johnson et al., 1999; Hanenberg, et al., 2001; Knol, 2001; Lund et al., 2002).

In addition to low heritabilities and unfavorable genetic correlations, it should be noted that the number of parities produced or length of productive life is a trait directly measured on only females and can only be recorded after a sow has been culled at the end of her productive life (at culling or death). Therefore, the selection for longevity may be more effective through indirect selection e.g. through leg conformation or some other indicator trait. The heritability estimates for leg conformation traits have ranged from 0.01

to 0.39 in the studies by Webb et al. (1983), Lundeheim (1987), Jörgensen and Vestergaard (1990), Huang et al. (1995), and López-Serrano et al. (2000). López-Serrano et al. (2000) reported also that the genetic correlation between leg conformation and longevity was close to zero in Large White, and moderately favorable in Landrace populations. Thus, the indirect selection potential for longevity through improvement of leg conformation may be population dependent.

1.2 Selection for sow efficiency in Finland

In Finland, pig breeding is based on a national program, where the two equally popular breeds, Landrace and Large White, have been under the same breeding objectives since the beginning of 20th century (Maijala, 1999). Currently, there are three types of testing methods: station testing, on-farm testing, and litter recording. Both the station and on-farm testing have been developed primarily for genetically improving on production traits, such as daily gain, feed conversion ratio, carcass quality and meat quality. Information on leg conformation traits is collected at the station and on-farm tests. The litter recording scheme is focused on collecting information on sow efficiency traits. At a member farm in the litter recording scheme, total number of piglets born, number of stillborn piglets and farrowing date are recorded. In majority of these cases (~95 %), the number of weaned piglets and weaning date are recorded. The litter recording scheme also provides the reason and date of culling for all sows removed from the farm.

The national program provides plenty of information for selection with relatively low costs. There are annually some 60 000 sows in the litter recording scheme. Approximately one third of the sows are Landrace, one third are Large White, and the remaining are Landrace x Large White (F_1) crosses. Using these results, BLUP breeding values for prolificacy traits have been obtained since 1991 (Mäntysaari, 1992). The index, introduced in 1991, contained total number of piglets born (80 % weight) and farrowing interval (20 %). The breeding values were estimated using a single trait repeatability model.

1.3 Possibilities to improve breeding for sow efficiency in Finland

Although there is a plenty of information available for selection on sow efficiency, the prolificacy index mentioned above has traditionally been the only selection criteria for sow efficiency. Thus, there are several avenues remaining in which the Finnish program may be modified in order to improve the genetic gain for sow efficiency. First of all, both the direct and indirect (through leg conformation) selection potential for longevity should be studied. Similarly, the prolificacy index should be critically re-evaluated to ensure that the proper traits along with their index weights are implemented.

The expertise of Finnish pig breeders has been demonstrated by the rapid genetic improvement for the production traits. However, the genetic gain in the prolificacy traits under selection has not been as high as expected; actually farrowing interval has increased over time (FABA, 2002). Therefore, a question arises: how could the reliability of breeding value estimation of prolificacy traits be improved? In the case of low heritability traits, it is important to use all the information available. The sow efficiency traits are genetically correlated, i.e., multiple trait analysis should be carried out. Moreover, the possible associations between sow efficiency and production traits should be accounted for.

Zhang et al. (2000) reported that there is a favorable genetic correlation between daily gain and piglet mortality, whereas the correlation between backfat thickness and piglet mortality was unfavorable. Similarly Knol (2001) concluded that 'selection for increased pre-weaning survival will increase daily gain, feed intake and backfat'. Moreover, carcass quality has been reported to be unfavorably correlated with leg conformation traits (Webb et al., 1983; Jörgensen and Vestergaard, 1990).

The development of more accurate or detailed statistical models is another way to improve reliability of estimated breeding values. For example, although the effect of service sire on litter size appears to be low (Brandt and Grandjot, 1998; van der Lende et al., 1999), an evaluation should occur to determine whether or not it should be accounted for in the statistical models of breeding value estimation. Moreover, no consensus exists concerning the validity of using repeatability model in breeding value estimation of prolificacy traits. Roehe and Kennedy (1995) demonstrated that genetic correlations of litter size among different parities were low, hence different parity records should be considered as different traits. In contrast, Haley et al. (1988) concluded that records from different parities should be considered as repeated records, whilst Irgang et al. (1994), Rydhmer et al. (1995), Täubert, et al. (1998), Hermesch et al. (2000), and Hanenberg et al. (2001) suggested that the first and later parities should be treated as different traits, and the records from the second parity and onwards could be considered as repeated records.

1.4 Objectives of the study

The efficiency of a sow is a sum of prolificacy and longevity traits. These trait groups can be divided to several individual traits. The traits affecting prolificacy include age at first farrowing, farrowing interval, litter size and piglet mortality. Similarly, the selection for longevity can be carried out directly through the evaluation of length of productive life or some similar measure, or indirectly by selection for leg conformation. Although sow efficiency is a sum of many characters, BLUP index for prolificacy has traditionally been the only selection criteria for sow efficiency. Thus, there seems to be several avenues that could be exploited in order to improve the efficiency in the Finnish pig breeding program. Therefore the objectives of this study were:

1. To determine the genetic variation for sow efficiency traits including prolificacy, longevity, and leg conformation.

2. To understand the co-responses (genetic correlations) among sow efficiency traits and other economically important traits including growth rate, feed conversion ratio, carcass quality, and meat quality.

3. To determine the feasibility of improving breeding value estimation of the sow efficiency traits.

The results from the current analyses can be used as guidelines in decision making when refining Finnish pig breeding program. Moreover, the (co)variance components can be utilized in practice when breeding value estimation of Finnish Landrace and Large White populations occurs.

2 Materials and methods

2.1 Data sets

To investigate selection potential, genetic associations, and feasibility of improving breeding value estimation of the different Finnish sow efficiency related traits, five separate studies were carried out. In the studies I, IV, and V, selection potential of the different prolificacy and longevity traits were studied. In the current thesis, an efficient female is defined as sow that produces many large litters without problems in conceiving and piglet mortality. The sow efficiency related traits studied are presented in Figure 1.

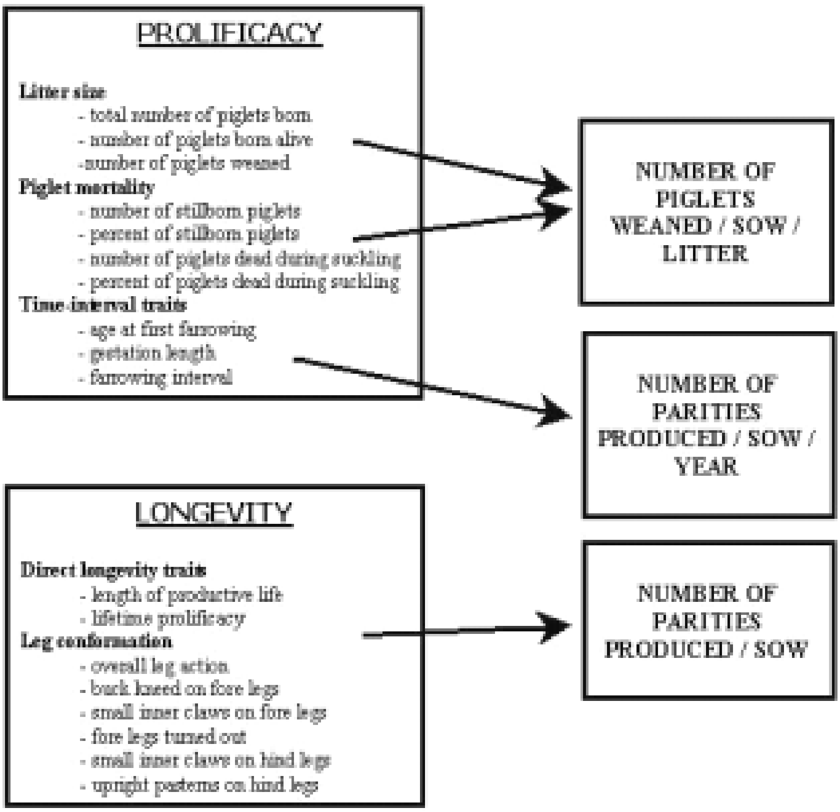


Figure 1. Summary of sow efficiency related traits and trait groups studied with their main breeding objectives.

Genetic associations were studied among the individual sow efficiency traits and between the sow efficiency and production traits (daily gain, feed conversion ratio [feed units / kg of daily gain], lean meat percent, fat percent [station test, III], backfat thickness [on-farm test, V], and pH and L* (luminance, measured with Minolta CR 300; CIE, 1971) values measured at the last rib of *longissimus dorsi* and lateral area of *semimembranosus* muscles). Moreover, genetic correlations between the records of the "same trait" at different parities were estimated to investigate whether repeatability model is valid in the breeding value estimation of litter size and farrowing interval.

All of the analyses carried out were based on purebred Landrace and Large White pigs and litters, and the data sets were obtained from the Finnish Animal Breeding Association (FABA). Three types of data sets were used (Figure 2). In III and IV, performance, leg conformation, meat quality, and carcass quality records were obtained from the Finnish test station system, whereas the information in V was obtained from the on-farm test. The data containing prolificacy information were extracted from the Finnish litter recording scheme.

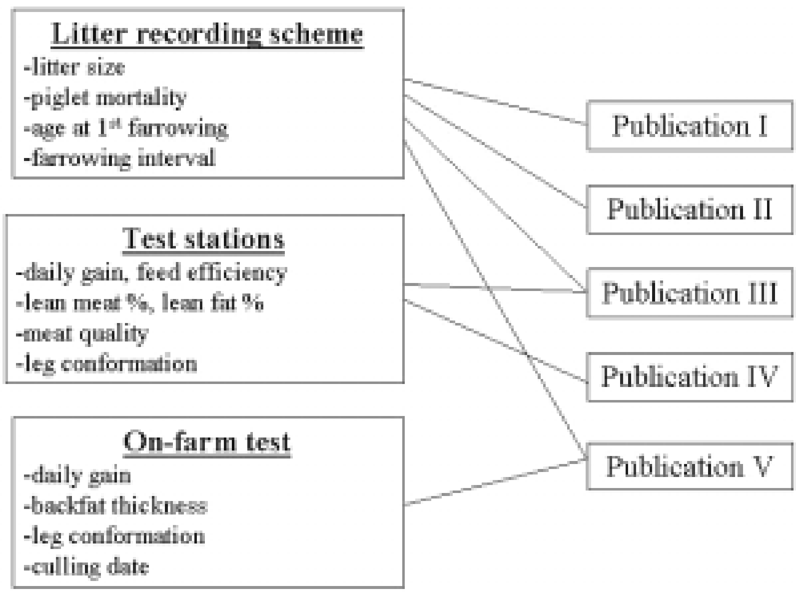


Figure 2. The use of different data sets in the papers I-V. The litter recording scheme and on-farm test traits were treated as sow traits, whereas sib test information was available only for their daughters and other relatives. Lean meat-%, lean fat-% and meat.

The information in the station testing data set consists of records collected from six sibling testing and one performance testing station. The latter was used only in IV. The test period was from 30 kg to 100 kg in the sibling test, and from 25 kg to 100 kg in the performance test. The sibling test group consisted of three full-sibs. Until 1999 (I), sibling makeup was 1 castrate and 2 females or 2 castrates and 1 female in the test group. Since 1999, it has been possible to test boars in the sib testing station. For the performance test, the test group consists from 1 to 3 full sib boars. At the on-farm test, the FABA breeding advisers performs the measurements (weight, backfat thickness, conformation) when the pig weighs approximately 100 kg

Meat quality traits were treated differently in III and IV. In IV, meat quality index was used, whereas the original meat quality records were used in III. The meat quality index combined pH (33% weight) and L* (66%) values measured on the *longissimus dorsi* muscle that was excised at the last rib and deviated from the slaughter day mean. The objective of using such meat quality index in the breeding scheme has been to keep meat quality constant in the Finnish pig populations. However, the difference between the studies is due to the changes in the selection program for meat quality in Finland. The studies in this thesis followed these practical breeding routines in the case of meat quality.

Because of the large amount of information from litter recording scheme, only records from the largest farms were utilized in the studies II, III, and IV. The farm size was used as a major criterion in sampling to avoid problems in estimating farm-year effects in the statistical analysis. In V, the information was utilized from farms that performed on-farm testing for the whole sow herd.

2.2 Statistical analyses

In I-IV, (co)variance components were estimated using the DMU package (Jensen and Madsen, 1994; Madsen and Jensen, 2000), which implemented Restricted Maximum Likelihood (REML) procedures. In V, the data were analyzed using both a survival analysis and linear model REML. Survival analyses were carried out using the Survival Kit package (Ducroq and Sölkner, 2001), and linear model analysis using the DMU package (Madsen and Jensen, 2000). An animal model was used in the analyses of the data sets in I-IV, and a sire model was incorporated in V.

The leg conformation traits have been scored by station manager (in test stations) or by breeding consultant (on-farm test). Because the score range for symptoms of leg weakness is different at the sib testing (1, 2, 3, 4) and performance testing (1, 2) stations, the observations were rescaled to frequency-normalized values in I. The frequency-normalized values were obtained as means of an underlying liability variable corresponding to the frequency (in sib or performance test) of the recorded value. The means (y_n) were calculated as showed by Lush (1948): $y_n = (z_n - z_{n-1})/(p_n - p_{n-1})$, where z_n is the height of the ordinate of the standard normal distribution, and p_n is the proportion of animals up to the n^{th} threshold.

In addition to fixed effects, the random effects of the animal (additive genetic effect), common litter, and residual were included in statistical models for symptoms of leg weakness in IV. The statistical model for the performance, carcass quality, and meat quality traits (in III and IV) were the same as those used in the breeding value estimation in Finland, containing additive genetic animal and residual effects as random effects. The additive genetic sire and residual effect were the random effects in the statistical model of on-farm test records in V.

The statistical models for the prolificacy traits were following the objectives of the studies I-III. To investigate the effect of service sire and validity of repeatability model in the breeding value estimation of litter size and farrowing interval, three different models were applied in II. When the records from different parities were treated as different traits, additive animal and residual were included as random effects in the statistical model. In addition, additive genetic and permanent environmental effects of service sire were included in the model of the first parity records of total number of piglets born. Moreover, random permanent effect of a sow was included in the repeatability analysis in study II. In studies I, III, and V, the main objectives were to investigate genetic potential of different prolificacy traits and genetic associations between the traits, and therefore, additive genetic sow and residual were the only random effects included in the statistical models.

In addition to (co)variance components, correlations between the estimated breeding values were calculated in II and V. This was carried out to investigate the effects of differences in breeding value estimation on the ranking of animals. In II, the differences in ranking by breeding value of young boars from litters born from 1998 and later were evaluated. In V, the same was done for all sires with at least one daughter having uncensored record in the studied data set.

3 Results

The phenotypic means of the sow efficiency traits were very similar in the two breeds. The average Landrace sow was 348 d, and Large White sow was 365 d old at the first farrowing. In the first parity, Landrace sows averaged 10.5 piglets born, from which 0.8 were born dead and 1.1 died before weaning. The corresponding numbers in Large White sows were 10.8, 0.9, and 1.2, respectively. The average first farrowing interval was 169 and 170 d in Landrace and Large White, respectively. In both breeds, the average length of productive life was 439 d (uncensored records), and the number of piglets born (alive) during that period was 32 in Landrace and 33 in Large White. Similarly, buck kneed (30 % in Landrace and 46 % in Large White) and small inner claws (20 % in Landrace and 21 % in Large White) on fore legs and small inner claws on hind legs (50 % in Landrace and 46 % in Large White) were equally common and the most severe symptoms of leg weakness in both breeds. Moreover, the average overall leg action scores (scored from 1 to 5) ranged from 2.86 to 3.57 in Landrace and 3.18 to 3.54 in Large White.

3.1 Variance components

In general, the estimated heritabilities were very similar in the different data sets (Table 1). The heritabilities were low for all of the sow efficiency traits, except for age at first farrowing (0.26 - 0.47), gestation length (0.25 - 0.37) and length of productive life in the survival analysis (0.16 - 0.19).

In litter size (total number of piglets born, piglets born alive, number of piglets weaned) and piglet mortality (number of stillborn piglets, number of piglets dead during suckling) traits, there was a tendency for the traits recorded at farrowing to have higher heritabilities than those recorded at weaning (I). Similarly, the heritability estimates for litter size and especially for farrowing interval were higher for first parity records (0.13 – 0.15 for litter size and 0.11 – 0.16 for farrowing interval) than for the later ones (0.11 – 0.13 for litter size and 0.00 – 0.07 for farrowing interval), or than for the estimates obtained using repeatability model (0.11 for litter size and 0.04 for farrowing interval) (II).

In addition to additive genetic effects, there was a clear permanent environmental effect over parities in litter size (repeatability = 0.18 in both breeds), and the proportion of variance due to common litter environment was at least as high as the heritability for leg conformation traits. The effect of service sire was small on litter size (0.01 – 0.03) and piglet mortality traits (0.01 – 0.04) (II, III). The heritability and service sire effects for piglet mortality were higher in Landrace than in Large White populations (I).

Table 1. Range of heritability estimates for sow efficiency traits in the studies I-V[1].

	Landrace	Large White
Prolificacy		
Litter size (TNB, NBA, NW)[2]	0.06 - 0.13	0.06 - 0.15
Piglet mortality (NSB, NSB-%, PM, PM-%)[2]	0.07 - 0.12	0.03 - 0.05
Farrowing interval	0.04 - 0.11	0.04 - 0.11
Age at first farrowing	0.26 - 0.47	0.32 - 0.39
Gestation length	0.25	0.37
Longevity		
Overall leg action score	0.06	0.06 - 0.07
Symptoms of leg weakness	0.05 - 0.20	0.03 - 0.16
Length of productive life	0.05 - 0.17	0.10 - 0.19
Lifetime prolificacy	0.09	0.12

[1] For litter size, piglet mortality and symptoms of leg weakness, the heritability has been presented for a trait group rather than for the individual traits themselves.

[2] TNB = total number of piglets born, NBA = number of piglets born alive, NW = number of piglets weaned, NSB = number of stillborn piglets, PM = piglet mortality during suckling

3.2 Correlations among sow efficiency traits

The summary of the magnitude and signs of genetic correlations among the sow efficiency traits is presented in Table 2. Among litter size related traits, there was unfavorable correlation between litter size at birth and piglet mortality. Thus, selection only for litter size at birth may lead to higher piglet mortality, and despite the genetic gain in litter size, the improvement in the number of piglets weaned would not always be obtained.

The genetic correlations between age at first farrowing and farrowing interval (0.25-0.74), and between age at first farrowing and gestation length (0.24-0.25) were moderate (I). The favorable genetic correlation between age at first farrowing and farrowing interval is beneficial for both the traits, but especially for farrowing interval. The age at first farrowing is moderately heritable, and through genetic correlations in multiple trait analyses, the reliability of estimated breeding values for farrowing interval should increase.

Among longevity traits, lifetime prolificacy and length of productive life are genetically similar traits, and both the genetic and phenotypic correlations between the traits were very high (>0.90) (V). This is reflecting the fact that the longer the sow remains in the herd, the greater the number of piglets she has potential to produce. Moreover, a moderately favorable genetic correlation between overall leg action score and longevity in Landrace was found (0.32) (V). The corresponding correlation in Large White was not so clear, as the standard error of the estimate (0.16) was almost as high as the estimate itself (0.17) (V).

Litter size (number of weaned piglets) and farrowing interval were also moderately genetically associated with length of productive life and lifetime prolificacy (V). The correlations may be partly explained by autocorrelation, as farmers do not keep sows producing small litters. Moreover, the farmer has been forced to remove sows that fail to come into oestrus. In any case, the relatively high genetic correlations are indicating that all the sow efficiency traits should be analyzed simultaneously in the BLUP breeding values estimation.

The genetic correlations among first and later parity litter size records (0.32 – 0.87) were lower than the correlations between later parity records (0.59 – 0.99) (II). Similarly, all genetic correlations for farrowing interval among different parities were lower than one. Thus, the current results suggests that the first and later parities of litter size, and all the parities of farrowing interval should be treated as separate traits in breeding value estimation.

Table 2. Signs and level of genetic correlations between the main sow efficiency traits in Landrace (upper triangle) and Large White (lower triangle) populations. The correlations between –0.10 and 0.10 are presented with 0. The correlations between 0.10 and 0.50 are presented with +, and between 0.50 and 1 are presented with ++. The corresponding negative correlations are presented with minuses. The superscripts indicates whether the correlations are favorable (F) or unfavorable (U).

	1	2	3	4	5	6	7
Prolificacy							
Litter size[1] (1)		+ U	0[4]	0	+ F	++ F	- U
Piglet mortality[2] (2)	+ U		0[4]	+ F	ne[3]	ne[3]	- F
Age at first farrowing (3)	- U	0[4]		++ F	+ U	+ U	- F
Farrowing interval (4)	- U	0[4]	+ F		- F	- F	- F
Longevity							
Length of productive life (5)	+ F	ne[3]	- F	- F		++ F	+ F
Lifetime prolificacy (6)	+ F	ne[3]	- F	- F	++ F		+ F
Leg score (7)	0	0	0	0	+ F	+ F	

[1] Total number born, number of born alive, and number of weaned piglets
[2] Number of stillborn piglets and piglet loss during suckling
[3] not estimated
[4] The correlation differed from zero, but the signs were different in number of stillborn piglets and piglet loss during suckling. See paper II.

3.3 Genetic correlations between sow efficiency and production traits

The genetic correlation between the two performance traits in test stations (daily gain and feed conversion ratio), and similarly, between two carcass traits (fat-% and meat-%) were highly negative. The genetic associations of daily gain and feed conversion ratio with the sow efficiency traits, and similarly, the genetic associations of fat-% and meat-% with the sow efficiency traits are very similar.

Among the production traits, carcass quality had strongest correlation with the sow efficiency traits – unfortunately most of the estimates were unfavorable. Although most of the correlations had the same sign in both breeds, they were higher in Large White than in Landrace. Age at first farrowing, farrowing interval and leg conformation score were unfavorably associated with the carcass quality in both breeds. In addition, length of productive life, lifetime prolificacy, litter size, and piglet mortality had unfavorable correlations with the carcass quality in Large White.

In general, there was a tendency for performance and sow efficiency traits to be favorably rather than unfavorably associated. For example, there was negative genetic correlation between piglet mortality and performance traits measured at test stations (daily gain between 30 and 100 kg, and feed conversion ratio during that period). This indicates that high growth potential and feed efficiency are beneficial for the piglet already at birth. Moreover, age at first farrowing was favorably associated with daily gain in on-farm test. The corresponding correlation with daily gain recorded at test stations was close to zero. No clear associations were found between sow efficiency and meat quality traits.

4 Discussion

The objectives of this study were to determine the selection potential, genetic associations, and feasibility of improving breeding value estimation of the different sow efficiency related traits. To meet the objectives, genetic parameters of sow efficiency and genetic correlations between sow efficiency and the other traits included in the Finnish pig breeding program were estimated.

Because the farms are relatively small in Finland, the data was formed so that the number of observations in each farm-year sub-class was large enough to obtain reliable estimates for these contemporary groups. Therefore, farm size was the main criterion in sampling prolificacy data. However, the phenotypic distribution of the traits studied in papers I-IV were very similar to the corresponding distribution of the Finnish pig populations estimated by FABA (2002). Thus, it can be concluded that the current data sets were representative of the Finnish Landrace and Large White sow populations, except in V.

In V, the records were utilized only from farms that perform on-farm test on all sows. Because of that, the information of V was obtained largely from breeding farms. Therefore, the cumulative percentages of culling over parities were higher than those of typical of average of whole Finnish pig populations (Figure 2). Thus, the data set of V represents Finnish breeding sows rather than average Finnish sows.

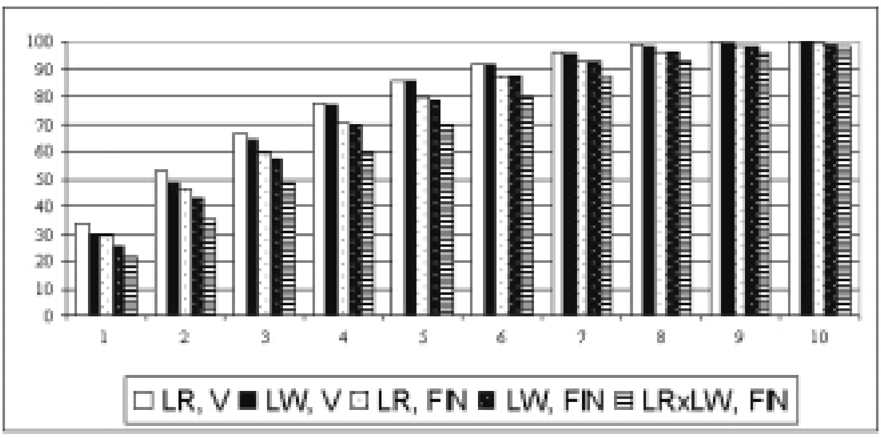


Figure 3. Cumulative percentages of culling over parities in Landrace (LR) and Large White (LW) sows in the data set of V and in the whole data set of Finnish litter recording scheme (FIN).

A linear model was applied for the analysis of leg conformation and prolificacy traits. However, many of the traits were of a categorical nature. For such categorical traits, the application of threshold model would theoretically be more appropriate (Gianola, 1982). However, it is well known that heritability estimates obtained using linear model are underestimated from those on the liability scale, and the magnitude of underestimation is dependent on the frequency of the symptom (Dempster and Lerner, 1950). Moreover, according to the simulation study by Mäntysaari et al. (1991), the estimated genetic correlations from linear model analysis of binary trait are close to the true values. Thus, although the application of a threshold model would be theoretically more valid than linear model in the analyses of categorical characters, it can be concluded that the results of the present study are valid.

4.1 Selection potential of sow efficiency traits

4.1.1 Litter size

The estimated heritabilities for litter size traits in the current analyses ranged from 0.06 to 0.15 (Table 1), being of the same magnitude as those presented in the literature (Southwood and Kennedy, 1990; Estany and Sorensen, 1995; Roehe and Kennedy, 1995; Rydhmer, 2000; Hanenberg, et al., 2001). Similarly, the heritability of the litter size traits tended to decrease when the trait was more dependent on piglet mortality (h^2 estimates were highest in total number of piglets born and lowest in number of piglets weaned) (I) is also in agreement with other studies (Southwood and Kennedy, 1990; Adamec and Johnson, 1997).

An unfavorable correlation between litter size at birth and piglet mortality was found. Thus, selection only for litter size at birth may lead to higher piglet mortality. Unfavorable genetic correlations between litter size and piglet mortality have been reported also in previous studies (Hanenberg, et al., 2001; Knol, 2001). Similarly, the selection for total number of piglets born has resulted in higher unfavorable genetic change in number of stillborn piglets (1.56) than the favorable increase in number of piglets born alive (0.88) in the selection study by Johnson et al. (1999).

The heritability estimates for the piglet mortality traits ranged from 0.03 to 0.12 (Table 1). The heritability estimates, and similarly the estimates on the proportion of variance due to the service sire effect, were higher in Landrace than in Large White population. The difference is in agreement with the study by Lund et al. (2002), which was based on Finnish Landrace and Large White data. Their heritability estimate (as a sow trait) for proportion of weaned piglets out of born alive was 0.08 in Landrace and 0.01 in Large White population. Similar variation in heritability estimates for the piglet mortality traits has been seen in other populations (Van Arendonk et al., 1996; Hanenberg et al., 2001; Grandinson et al., 2002). In any case, based on heritability estimates, a greater selection response for piglet mortality in Landrace than in Large White population could be expected.

Although the estimated heritabilities are low, it is possible to obtain genetic gain in litter size and piglet mortality in an efficient breeding program. However, the selection should be practiced simultaneously for litter size and against piglet mortality, i.e., the unfavorable genetic correlations between litter size and piglet mortality should be taken into account. In the other words, selection should be for number of weaned piglets, either directly or indirectly by selecting for high total number of piglets born and for low piglet mortality (both during farrowing and until weaning).

4.1.2 Age at first farrowing and farrowing interval

The heritability estimates for the age at first farrowing, farrowing interval and gestation length indicate that there are opportunities to decrease costs of piglet production by genetically improving these traits by selection (Table 1). The heritability estimates for the age at first farrowing and gestation length are high for prolificacy traits. The moderate heritabilities for age at first farrowing and gestation length are in agreement with the review by Rydhmer (2000) and in later the study of Hanenberg et al. (2001).

The heritability was higher for the first farrowing interval than for the later ones, or than for the estimates obtained using repeatability model (II). After the first two farrowing intervals, the heritability for the farrowing interval is very low, and thus, possibilities to obtain selection response is very limited as well. Heritability estimates for farrowing interval have been reported to be lower than 0.10 (Rydhmer et al., 1995; Tholen et al., 1996a), and are similar to the estimates in the current study.

The genetic correlation between age at first farrowing and farrowing interval is beneficial for both the traits, but especially for farrowing interval. Because age at first farrowing is moderately heritable, the reliability of estimated breeding values for farrowing interval should increase as a result of the favorable genetic correlations that exist between the two traits when conducting multiple trait analyses. More generally, the breeding objective for traits measuring time intervals is to increase number of litters produced per sow per year, i.e., one would like to shorten the intervals between and before farrowing. However, there is moderate negative genetic correlation between gestation length and piglet mortality during suckling (I; Hanenberg, et al., 2001). In addition, the genetic variation of gestation length is very small, and hence the selection response in the number of litters per year may be very small. Therefore, the advantage of breeding for short gestation length is not obvious. On the contrary, it might be more effective to select for longer gestation length, which would be an indirect selection for low piglet mortality.

Age at first farrowing was correlated differently with litter size and piglet mortality. Age at first farrowing had either zero (total number born, number weaned) or negative (number born alive) correlation with litter size in Landrace, whereas the corresponding correlations were positive in Large White. Similarly, there was no significant genetic correlation between age at first farrowing and the piglet mortality traits in Large White, whereas number of stillborn piglets was favorably correlated, and piglet mortality during suckling unfavorably correlated with age at first farrowing in Landrace. Thus, based on these correlation estimates, it seems easier to obtain simultaneous genetic response in age at first farrowing and number of piglets weaned in Landrace than in Large White swine.

4.1.3 Longevity

The heritability estimates for length of productive life were lower when estimated using linear model when compared to survival analysis (0.16-0.19). This is in agreement with the literature. The earlier estimates of the heritability for stayability, analyzed using linear model, have ranged from 0.02 to 0.11 (Tholen et al., 1996a, 1996b; López-Serrano et al., 2000), while the survival analyses estimates for length of productive life have ranged from 0.11 to 0.31 (Yazdi et al., 2000a, 2000b). The difference in the estimates indicates that environmental effects are modeled more accurately in survival analysis than in linear model analysis. This is most likely attributable to the ability to model farm-year effect as a time dependent variable. Moreover, it is possible to account for censored records (sow still alive, remained in the herd at least X days) in the survival analysis.

Favorable genetic correlation between overall leg action score and length of productive life indicates that overall leg conformation scored at 100 kg can be used as an early predictor for future leg problems (V), especially in Landrace sows. In the Large White breed, the association was not so clear, as the standard error of the estimate (0.16) was almost as high as the estimate itself (0.17). Similarly in the study by López-Serrano et al. (2000), the genetic correlation between stayability and leg score was positive in Landrace, and close to zero in Large White.

Although the genetic correlation between leg conformation score and length of productive life is favorable, one has to keep in mind that the heritability for leg conformation score ranged from 0.06 to 0.07 (IV, V). Among the different symptoms of leg weakness, buck kneed on fore legs (0.14-0.19) and small inner claws on hind legs (0.07-0.18) had the highest heritabilities (IV). Moreover, buck kneed on fore legs is highly genetically correlated with overall leg action. This is in agreement with the correlation estimates obtained by Webb et al. (1983) and Jörgensen and Vestergaard (1990). Thus, the reliability of breeding value estimation for leg conformation score might be improved by utilizing information on buck kneed on fore legs in a multiple trait analysis.

Most of the earlier heritability estimates for leg conformation traits are higher than the current estimates (Bereskin, 1979; Jörgensen and Vestergaard, 1990; Huang et al., 1995; Stern et al., 1995; López-Serrano et al., 2000). However, Webb et al. (1983) found values of a similar magnitude as those from the current analyses. Moreover, the earlier heritability estimates have been associated with reasonably high standard errors (Bereskin, 1979; Huang et al., 1995), and there were studies where the common environmental effect had not been accounted for in the statistical model (Jörgensen and Vestergaard, 1990; Stern et al., 1995). Moreover, the comparison of genetic parameters of threshold traits from different populations may be misleading, because the estimates are functions of the incidence rate (Dempster and Lerner, 1950).

In Finland, there has been discussion about changing leg scoring from the current (more or less binary trait) to a “linear scoring” system. In the “linear scoring”, each individual and each trait must be scored with a wider range of scores. Using this approach, one would expect higher heritability estimates for leg conformation traits, because variation in the traits is more effectively recorded (Thompson et al., 1981, 1983). In practice, such a linear scoring has produced higher heritabilities in horse populations (Van Bergen and Van Arendonk, 1993; Koenen et al., 1995). Similarly, López-Serrano et al. (2000) found 13 % heritability for leg score in on-farm tested pig populations. In their data set, the leg score was scaled on a more linear scale of 1 to 9.

4.2 Genetic correlations (r_g)

4.2.1 r_g between prolificacy and longevity traits

Litter size (number of weaned piglets) and farrowing interval have a moderate genetic correlation with length of productive life and lifetime prolificacy. Although the correlations may be partly explained by autocorrelation, they are indicating that all the sow efficiency traits should be analyzed simultaneously in the BLUP breeding values estimation. Stayability has also previously been genetically correlated with litter size and farrowing interval (Tholen et al., 1996b). Similarly, Yazdi et al. (2000 a,b) reported that sows with small litters have higher risk of being culled when compared to sows with larger litters. Moreover, they reported that high age at first farrowing increases the probability of being culled. In the current analysis, the genetic correlation between age at first farrowing and length of productive life (and lifetime prolificacy) was positive in Landrace and negative in Large White.

There is a common belief among producers that sows without leg problems crush a lower percentage of their piglets during lactation, i.e., there should be favorable association between leg conformation of the sow and piglet mortality (when measured as a sow trait). However, no clear genetic interactions were found between prolificacy and leg conformation traits in the Finnish Landrace and Large White populations (III). Thus, current analyses do not support the belief that leg conformation and piglet mortality are genetically associated. However, the current analyses did not have power to refute environmental (and phenotypic) correlation between piglet mortality and leg conformation.

4.2.2 r_g between sow efficiency and production traits

The generalization of genetic correlations of sow efficiency with the performance, carcass and meat quality traits are presented in Figure 4. In general, there was a tendency that performance traits were favorably and carcass quality traits unfavorably correlated with sow efficiency. No clear associations were found between sow efficiency and meat quality traits.

r_g between sow efficiency and performance

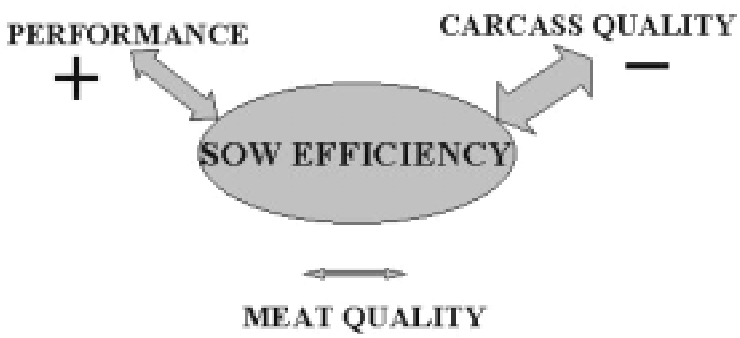
In general, there was a tendency for performance and sow efficiency traits to be favorably rather than unfavorably associated. For example, there was favorable genetic correlation between piglet mortality and performance traits measured at test stations (daily gain between 30 and 100 kg, and feed conversion ratio during that period). This indicates that high growth potential and feed efficiency are beneficial for the piglet already at birth. These correlations are in agreement with those presented by Zhang et al. (2000) and Knol (2001).

Although the general tendency in the genetic correlations between the performance and the sow efficiency traits is favorable, there were also unfavorable correlations, especially in Large White population. For example, there was unfavorable correlation between daily gain and overall leg action score in the on-farm test data set, and similarly between buck kneed on fore legs and daily gain in the station test data set in the Large White population. The corresponding correlations were close to zero in the Landrace population. Similarly, unfavorable correlations were found between total number of piglets born and the performance traits in Large White, while they were close to zero in Landrace. Moreover, the number of piglets weaned was favorably correlated with daily gain recorded at the on-farm test in Landrace, whereas the corresponding correlation was close to zero in Large White. The current results are in agreement with the literature, where many studies have concluded that there is zero or only slightly unfavorable correlation between litter size and performance traits (Rydhmer et al., 1995; Estany et al., 2002a; Noguera et al., 2002; Chen et al., 2003).

The correlations between daily gain and age at first farrowing differed between the station test and the on-farm test data sets. The genetic correlation was close to zero in the station test, whereas it was favorable in the on-farm test. Moreover, the unfavorable genetic correlation between age at first farrowing and carcass quality was lower in the on-farm test data set than in the station test data set. These differing results appear to have a reasonable explanation. First of all, the genetic trend in daily gain between 30 and 100 kg has been very high, and at the same time age at first farrowing has increased (FABA, 2002). The changes are indicating that daily gain between 30 and 100 kg and age at first farrowing may not be highly genetically associated. On the other hand, it is plausible that sows with superior growth rate will reach puberty at an earlier age, and thus, the correlation between daily gain and AFF should be negative, i.e., favorable. Moreover, also Rydhmer et al. (1995) showed that the genetic correlation between age at first farrowing and daily gain was moderately or highly negative.

There are two natural explanations for the correlation differences discussed in the previous paragraph. First of all, there may be differences in feeding strategies used at the test stations and at the farms. It is well known that the correlation between backfat thickness and daily gain is favorable when pigs are raised using a restricted feeding, and unfavorable when pigs are given *ad libitum* access to feed (Clutter and Brascamp, 1998). In the test stations, restricted feeding is practiced, whereas farmers are advised to provide gilts *ad*

Figure 4. Generalization of the associations between sow efficiency and production traits obtained in studies III, IV and V. Favorable associations are signed with + and unfavorable with -.



libitum or close to *ad libitum* access to feed (Puonti, personal communication). However, it is not well known whether farmers follow these recommendations, and therefore this explanation is not certain. In addition to possible differences in the feeding, it should be remembered that daily gain is measured between 30 and 100 kg in the test stations, and between birth and 100 kg in the on-farm test, i.e., the growth between birth and 30 kg is also affecting some variation on average daily gain. All in all, the difference can most likely be explained by the fact that daily gain recorded during station test and on-farm test are not controlled entirely by the same genes.

r_g between sow efficiency and carcass quality

Among the production traits, carcass quality had strongest correlation with the sow efficiency traits – unfortunately most of the estimates were unfavorable. That is very undesirable, because carcass traits are economically one of the most important traits of pork production (Ollivier, 1998).

Although the correlations between age at first farrowing and carcass quality was lower in the on-farm test (backfat thickness) when compared to the station test (meat-% and fat-%), both the data sets indicated that carcass quality is genetically correlated with age at first farrowing in an unfavorable manner. Thus, it seems that fat mass is the limiting factor for sexual maturity in the current Finnish Landrace and Large White populations. The present results are supported by the unfavorable genetic correlation between backfat thickness and age at first farrowing found in the study by Rydhmer et al. (1995). Thus, it seems that the increase in age at first farrowing in the Finnish pig populations is due to very successful selection for the carcass quality (FABA, 2002). To avoid the unfavorable trend in the future, selection for the low age at first farrowing should be practiced simultaneously.

The unfavorable correlations between carcass quality and sow efficiency traits are in agreement with the estimates presented in the literature. Webb et al. (1983), Rothschild et al. (1988), and López-Serrano et al. (2000) found carcass quality to be genetically unfavorably correlated with leg conformation and sows' stayability. Moreover, Zhang et al. (2000) and Knol (2001) found carcass quality to be unfavorably associated with piglet mortality.

r_g between sow efficiency and meat quality

In general, no clear association between sow efficiency and meat quality traits were found. Thus, simultaneous selection for both the traits is not likely to be impeded by any unfavorable associations. Similarly, meat quality and prolificacy traits were not associated in the studies by Hermesch et al. (2000) and Estany et al. (2002b). There were no other reported studies on correlation of meat quality with leg conformation or length of productive life.

Although there were no clear associations between meat quality and sow efficiency, it should be remembered that the correlations are changing due to selection. In the long run, simultaneous selection on two uncorrelated traits leads to unfavorable correlation due to faster fixation of favorable gene-pairs than unfavorable ones (Falconer and Mackay, 1996). In Finland, both total number of piglets born and meat quality have been under selection since 1990 and thus, unfavorable correlations may be expected to develop in the future.

4.3 Statistical models in the breeding value evaluation

The current results indicated that the assumptions of repeatability model are not fulfilled. Therefore, in the BLUP breeding value estimation, first parity litter size records should be treated as different traits than the records from later parities. Moreover, all the farrowing intervals should be treated as different records. The effect of accounting (or not) for service sire effects in the statistical model of litter size on ranking of AI-boar candidates is small. In the breeding value estimation of length of productive life, it is possible to model time-dependent effects and account censored records. However, the software available for survival analysis can only incorporate single trait models rather than the more desirable multiple trait models. Therefore, more research is needed to develop breeding value estimation for longevity analysis.

4.3.1 Prolificacy

Based on the results obtained in II, the ranking of AI-boar candidates is very similar whether or not the effect of a service sire is accounted for in the statistical model of litter size (correlation between pedigree index BLUP was 0.99 in Landrace and 1.00 in Large White). However, there were some differences in the ranking between multiple trait and repeatability model analysis, especially for farrowing interval. The correlations between pedigree indices were 0.94 and 0.88 in litter size and farrowing interval, respectively.

When applying a repeatability model, it is assumed that the genetic correlation between the repeated records is one, and the variance components are the same for all the parities. However, it seems that the litter size of first parity is at least partly controlled by different genes than litter size in later parities (II, Irgang et al., 1994; Roehe and Kennedy, 1995; Rydhmer et al., 1995; Täubert, et al., 1998; Hermesch et al., 2000; Hanenberg et al., 2001). Moreover, heritability for the first parity litter size records was higher than for the later parity records. For farrowing interval, the results were even more clear.

In general, it is concluded that the assumptions of repeatability model are not fulfilled, and thus different rankings are obtained with repeatability and multiple trait model.

The similarity between pedigree indices of AI boar candidates when the service sire effect is accounted for (or not) in the statistical model is also natural, because the effect of service sire on litter size is relatively small (II, See et al., 1993; Brandt and Grandjot, 1998; van der Lende et al., 1999). However, it should be remembered that the effect of service sire was clearly higher in the piglet mortality traits, especially in the Landrace breed (I). Moreover, there is always some culling of AI-boars due to small litters. Traditionally, this culling has been based on phenotypic averages. By including the effect of service sire in the statistical model of BLUP analysis, simultaneous estimates for service sire effects are obtained. These estimates would be more reliable when making culling decisions for AI-boars when compared to using only the phenotypic averages.

In the literature, there has been discussion that maternal effect of a sow should be accounted for in the breeding value estimation of litter size, because there is unfavorable genetic correlation between maternal and direct sow genetic effects (Irgang et al., 1994; Roehe and Kennedy, 1995, Alfonso, et al., 1997; Lund et al., 2002). However, maternal genetic effect is usually of the same magnitude as that of service sire. Therefore, one might expect only small effects on ranking of predicted breeding values if the maternal genetic effect is accounted for in the statistical model.

4.3.2 Longevity

In theory, one cannot deny the superiority of survival analysis in the modeling approach of longevity data. In survival analysis, it is possible to account for information from censored records and to model time dependent factors. Therefore, there was re-ranking of the breeding values of the sires of the sows with uncensored records, when survival analysis or linear model was applied. The correlations between the breeding values ranged between 0.40 and 0.72 (V).

Although it seems that survival analysis better fits longevity data when compared to the application of a linear model, it should be remembered that it is not possible to account for information from correlated traits using the available software developed for the survival analysis. In an efficient pig breeding program, AI-boars are selected with very short generation interval. Therefore, the selection for length of productive life must be carried out using pedigree information. The reliability of the pedigree index will likely be lower without the utilization of information from correlated traits. This highlights the importance of developing breeding value estimation for longevity evaluation using a multiple trait analysis.

In the literature, two possibilities to develop multiple trait analysis for longevity data have been presented. In a simulation study, Meuwissen et al. (2002) fitted repeatability model on the data set that contained binary records indicating whether some fixed parity has been reached. The approach sounds logical and easy to implement. Moreover, the reliabilities of estimated breeding values were very similar as those obtained using survival analysis. Thus, the approach may have potential for practical applications. On the other hand, it should be remembered that the simulated data set is always relatively simple, and therefore, more research is needed to determine if the repeatability model would work using actual rather than simulated longevity data.

An alternative way to develop multiple trait analysis with longevity traits is to utilize information from censored records in linear model analysis. Guo et al. (2001) used Bayesian methodology in analyzing lifetime prolificacy and length of productive life with a linear model that accounted for censoring. Although they did not compare these results with survival model analysis, the method seems promising. At least the estimated heritabilities (0.22 – 0.25) were higher than those obtained using linear model in the current analyses.

4.4 Implications and future prospects

Based on the results obtained from the current studies, the routine to evaluate genetic ranking based on BLUP-index for leg conformation has been implemented, and the prolificacy index has been updated for the Finnish evaluation system. Overall leg action score and buck kneed on fore legs are the traits included in the leg conformation index. In the updated prolificacy index, the selection emphasis has been placed on total number of piglets born, against number of stillborn piglets, and piglet loss during suckling, for lower age at first farrowing and for shorter farrowing interval. For litter size and piglet mortality traits, the first parity results and results from the later parities are treated as different traits. Similarly, only the first two farrowing intervals are evaluated, and they are treated as separate traits. Both the prolificacy and leg conformation traits are analyzed with multiple trait animal model BLUP.

Although the effect of service sire on estimated breeding values was small, it is included in the statistical model of litter size and piglet mortality. This is done because there is always some culling of AI-boars due to poor piglet production. Estimates of the service sire effect from BLUP analysis are an efficient tool for that purpose.

In addition to breeding values, all the effects in statistical model of BLUP analysis are solved simultaneously. In prolificacy trait analysis, farm and year combination is one of the effects in the statistical model. Basically, it is accounting for the management factors carried out with the individual farms. As a by-product of BLUP analysis, www (world wide web) -application has been developed to show the level and changes in prolificacy due to management factors in a farm under examination. For large farms, (over 20 farrowing records per three months), the year is divided to three month periods. To ensure the reliability of farm-year-season effect, such a division is not carried out for smaller farms.

In Figure 5, an example of possibilities to show “problems” in the production is presented. Although the piglet death before weaning in the example farm is lower than average in Finland (solutions are scaled to zero), it should be noted that there is some increase in piglet loss during late summer or autumn in each year. One explanation for this might relate to the problems in the ventilation of piggery (temperature increases in summer). Alternatively, the farmer may be too busy to treat weak piglets during the harvesting time.

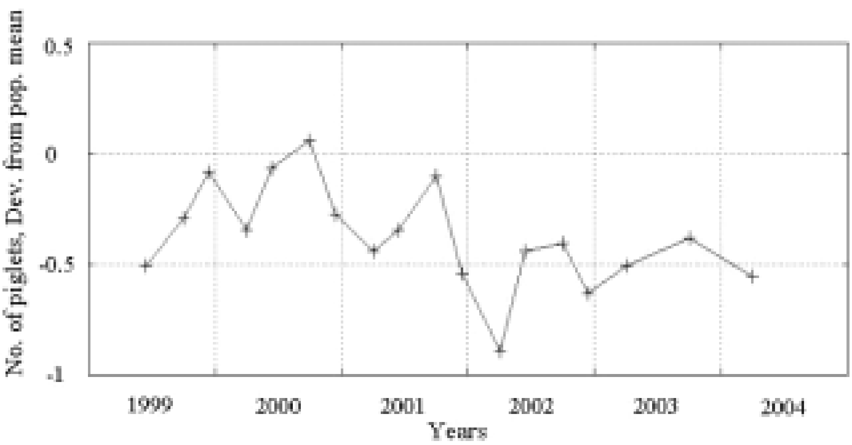


Figure 5. Farm-year solutions for piglet loss during suckling in the example Finnish swine farm.

Although the implementations described above have been carried out, the current results indicate that there are still avenues remaining in which improving the breeding routines for sow efficiency in Finland, especially with selection for longevity can occur. Because longevity is relatively strongly genetically associated with leg conformation and prolificacy (V), multiple trait analyses should be carried out in the breeding value estimation of longevity, leg conformation, and prolificacy traits. Currently, there is no breeding value estimation routine for longevity in Finland, and the prolificacy and leg conformation traits are analyzed separately. Moreover, the implemented leg conformation index is based only on station test information. Much information on leg conformation traits has been (and will be) collected in on-farm test. Because of uncontrolled pre-selection of tested animals in on-farm testing situations, it has not been possible to implement BLUP-index utilizing on-farm test records (Nylander et al., 1991). Therefore, more research is needed to avoid the problems relating to the use of pre-selected data on BLUP breeding value estimation. At least information from farms that are testing all their sows should be utilized in the breeding value estimation.

The results in IV and V indicate that production and sow efficiency traits are genetically associated. Therefore, breeding values for production traits should be analyzed simultaneously with sow efficiency traits. Thus, it is concluded that all the traits in the Finnish breeding program should be analyzed together. With the current set of traits and trait definitions, this results in a 23 trait animal model BLUP. Although it is computationally a big task, it should not be impossible with current computer software and hardware capacity.

It should also be remembered that the current study deals only with the selection potential and genetic parameters of different sow efficiency traits. Naturally more research is needed to evaluate the economic and social values of each trait in the Finnish pork production industry. Based on current results and economic calculations, it is possible to determine the traits, and their relative weights, that should be included in the total merit index.

5 Summary and conclusions

- Sow efficiency related traits are generally lowly heritable. The only exceptions are buck kneed on fore legs, age at first farrowing and gestation length, which are moderately heritable. The low heritabilities highlight the importance of using all the available information (volume of data, genetic correlations) in breeding value estimation.

- Litter size and piglet mortality are genetically unfavorably associated. Therefore, selection should be practiced simultaneously for litter size and against piglet mortality.

- The assumptions of repeatability model are not fulfilled in the case of litter size and farrowing interval. First and later parity litter size records should be treated as different traits in the breeding value estimation. Similarly, all the farrowing intervals should be treated as different traits.

- Age at first farrowing and farrowing interval are genetically favorably correlated. That is beneficial, especially for farrowing interval which is a lowly heritable trait.

- Prolificacy and leg conformation traits are favorably correlated with length of productive life and lifetime prolificacy. This highlights the importance of developing breeding value estimation for longevity analysis using a multiple trait analysis.

- In general, performance traits were favorably and carcass quality traits unfavorably correlated with sow efficiency, whereas clear associations were not found between sow efficiency and meat quality traits.

- Based on current results, BLUP-index for leg conformation has been implemented, and the prolificacy index has been updated for the Finnish evaluation system. Moreover, www-application has been developed to show the farm-year-season solutions from BLUP analyses to the farmers.

All in all, the current results have demonstrated that it is possible to obtain genetic gain for sow efficiency, with the use of an efficient breeding program. However, the sow efficiency traits are poorly heritable. That highlights the importance of accounting for all the information available using large data sets and correlations between various traits in multiple trait breeding value estimation in order to obtain the most accurate breeding values and make the most rapid genetic progress possible for the economically important traits evaluated.

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