Variance components for litter size and survival in Danish Landrace and Yorkshire pigs

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Abstract

Selection for total number of piglets born (TNB) since 1992 has led to a significant increase in this trait in Danish Landrace and Yorkshire, but has also resulted in an increase in mortality. The objective of this study was to estimate genetic and phenotypic parameters for litter size and survival in order to find alternative selection criteria to improve litter size at weaning. Data from Landrace (5178 litters) and Yorkshire (3938 litters) were analysed using REML based on a linear model including genetic effects of sow and service-sire. The estimates of heritability (based on the sow component) for TNB, number born alive (NBA), number alive at 5 days after birth (N5d) and at 3 weeks (N3w) were 0.081, 0.096, 0.109 and 0.111 in Landrace and 0.065, 0.080, 0.106 and 0.105 in Yorkshire. Genetic correlations between TNB and N3w were 0.39 in Landrace and 0.72 in Yorkshire, but between N5d and N3w the estimated genetic correlation was 0.99 in both lines. A preliminary analysis was conducted to estimate genetic parameters for survival rates by assuming the traits as Gaussian traits. The approximated estimates of heritability for survival rate per litter at birth (SVb), from birth to 5 days (SVb_5d) and from 5 days to 3 weeks (SV5d_3w) were 0.127, 0.127 and 0.016 in Landrace, and 0.073, 0.043 and 0.009 in Yorkshire. Genetic correlations between TNB and survival rates at different stages were negative in Landrace but erratic in Yorkshire. The results suggest that selection for N5d would be an interesting alternative to improve litter size at weaning.

Key words: pig, litter size, survival, heritability, genetic correlation

Introduction

Litter size at weaning is one of the most important traits in pig production. This trait can be considered as a complex trait involving ovulation rate, fertilization rate, prenatal survival rate and pre-weaning survival rate. Genetic improvement on any one of these component traits is expected to increase litter size at weaning.

In practical pig breeding, selection for litter size at birth is usually applied to improve litter size at weaning. Many studies have shown that the genetic correlation between litter size at birth and litter size at weaning is high (Strang and King, 1970; Johansson and Kennedy, 1985; Kaplon et al, 1991) because of the whole-part relationship. On the other hand some studies have reported an unfavourable correlation between litter size and survival rate. Robinson and Quinton (2002) reported a positive genetic correlation (0.50) between number of piglets born and number dead at birth (stillborn and neonatal death). Similarly Lobke et al. (1983) estimated the genetic correlation to be 0.54 between number of piglets born and number stillborn. Lund et al. (2002) reported a negative genetic correlation between total number born and survival rate at birth, and between total number born and survival rate from birth to weaning. Johnson et al. (1999) reported a lack of positive response for number of piglets weaned after 11 generations of selection for ovulation rate and embryo survival rate and after 3 generations of selection for total number of piglets born.

Direct selection for litter size at weaning should result in a direct improvement on the trait and an overall improvement of the component traits. However this approach could be restricted in practice due to practice of cross-fostering. Cross-fostering procedures are very widely applied in commercial pig production to increase survivability and growth of the piglets by uniforming the size of the litter reared. Cross-fostering makes it difficult to adequately estimate genetic parameters for litter size at weaning.

Litter size, prenatal survival and pre-weaning survival are usually treated as traits of the sow. However the fertilization capacity of the service-sire and the genotype of the piglet is likely to have an effect on these traits. Evidence supporting the relevance of the piglet's genotype on litter size was shown with an increase of about 0.3 in litter size in crossbred litters (Hill and Webb, 1982). Previous studies showed that the service-sire accounted for 0 - 5% of the total variance for litter size and for survival rate (e.g., Strang, 1970; See et al., 1993; Woodward et al., 1993; Van Arendonk et al.,1996; Van der Lende et al., 1999). It seems reasonable to estimate genetic parameters for these traits based on a model including both sow and service-sire genetic components.

Selection for total number of piglets born since 1992 has led to an increase in this trait in Danish Landrace and Yorkshire, but also to an increase in mortality. This could be due to a correlated response in piglet mortality, or due to a phenotypic relationship between litter size and mortality involving feed-back mechanisms (Gianola and Sorensen, 2004). The objective of this study is to present estimates of genetic and phenotypic parameters for litter size and to report preliminary results involving survival, in order to explore alternative selection criteria to improve litter size at weaning.

Materials and methods

Populations and data

Data were collected from 43 nuclear farms of Danish Landrace and Danish Yorkshire during the period from May 2002 to December 2003. Only records of pure-bred litters were used in the present study. Pedigrees for sows and sires were traced back to at least 5 generations. The structure of the data set is shown in Table 1. Sows were kept under commercial conditions and all matings took place using AI. At farrowing, the total number of piglets born and the number of dead piglets (stillborn and dead at birth) were recorded. Piglets were weighed individually within 2 days after farrowing. Piglet mortality, weight and the cause and date of death were registered during the pre-weaning period. Litter weight was recorded at weaning (average 21.37 days; range 19 – 23 days).

Table 1. Number of farms, sows, service-sires, litters, total piglets and the piglets involving in cross-fostering (CF-piglets)

Breed	Farm	Sow	Sire	Litter	Piglet	CF-piglet
LL	22	4421	971	5178	73697	6428
YY	21	3361	953	3938	51239	3031

Assignment of cross-fostering was done within the first three days after birth, and information concerning donor and recipient dams was recorded. In total there were 8.7% cross-fostered piglets in Landrace and 5.3% in Yorkshire. Fifty percent of the litters in Landrace, and 40% in Yorkshire were involved as either donors or recipients. The traits analysed were total number of piglets born (TNB), number of piglets born alive (NBA), litter size at 5 days (N5d), litter size at 3 weeks (N3w), survival at birth (SVb), survival from birth to 5 days (SVb_5d) and survival from 5 days to 3 weeks (SV5d_3w). N5d and N3w were measured on the basis of the number of piglets of the biological sow ignoring cross-fostering. SVb_5d and SV5d_3w were calculated on the basis of the number of piglets remaining in their own litter.

Statistical analysis

Litter size at different stages was analyzed using a two-trait model including sow and service-sire genetic effects as well as sow permanent effects,

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{W}_c\boldsymbol{c} + \boldsymbol{W}_{pe}\boldsymbol{p}_e + \boldsymbol{Z}_d\boldsymbol{d} + \boldsymbol{Z}_s\boldsymbol{s} + \boldsymbol{e}$$

where **y** is the vector of observations of litter size, **b** is the vector of fixed effects including farm, year-season and parity, **c** is the vector of random effects of farm-year-season, $\mathbf{p_e}$ is the vector of sow permanent effects, **d** was the vector of genetic effects of sow, **s** was the vector of genetic effects of service-sire, **e** is the vector of random residuals, and **X**, $\mathbf{W_c}$, $\mathbf{W_{pe}}$. $\mathbf{Z_d}$ and $\mathbf{Z_s}$ are design matrixes associating **b**, **c**, $\mathbf{p_e}$, **d** and **s** with **y**. In the model, the random effects were assumed to be independent of each other except **d** and **s** which were assumed to be correlated.

All random effects were assumed to be normally distributed,

$\mathbf{c} \sim \mathrm{N}(\mathbf{0}, \mathbf{I}\sigma_c^2)$, $\mathbf{p_e} \sim \mathrm{N}(\mathbf{0}, \mathbf{I}\sigma_{pe}^2)$, $\begin{bmatrix} \boldsymbol{d} \\ \boldsymbol{s} \end{bmatrix} \sim N\left(\mathbf{0}, A\begin{bmatrix} \sigma_d^2 & \sigma_{ds} \\ \sigma_{ds} & \sigma_s^2 \end{bmatrix}\right)$, and $\mathbf{e} \sim \mathrm{N}(\mathbf{0}, \mathbf{I}\sigma_e^2)$,

where σ_c^2 is variance of herd-year-season effects, σ_{pe}^2 is variance of permanent effects of sow, σ_d^2 is variance of sow genetic effects, σ_s^2 is variance of service-sire genetic effects, σ_{ds} is the covariance between sow and service-sire genetic effects, σ_e^2 is residual variance, **I** is identity matrix and **A** is the matrix of genetic relationship between animals in the pedigree.

A preliminary analysis of survival rate in different periods was conducted using the above model. The analysis was also carried out in the arc sine scale, $y_t = \arcsin(\sqrt{y})$, which is the classical transformation for binomial proportions. Inferences were almost identical, therefore we present results based on the original scale only.

The analyses were performed using the average information restricted maximum likelihood procedure (AI-REML) (Jensen et al., 1997) and using the DMU package (Madsen and Jensen. 2000).

Results

The mean and coefficient of variation for litter size and survival rate at different ages are shown in Table 2 and the distribution of mortality in different time periods is shown in Figure 1. Both populations showed a high TNB and high total mortality (31% in Landrace and 26% in Yorkshire). Landrace had a larger TNB but also showed higher mortality at birth than Yorkshire. As a result, NBA turned out to be similar in the two populations. Pre-weaning mortality was almost the same in the two populations with most deaths occurring during the first 5 days after birth. N5d and N3w in Landrace were similar to those in Yorkshire. Among the piglets dead at farrowing, 84% were stillborn and 16% died of other causes. Among the piglets died after birth, 32.5% were crushed, 23% died of starvation, 44.5% due to other causes. Coefficients of variation for litter size ranged from 25% to 31%, and had a tendency to increase with age. Coefficients of variation for SVb and from SVb_5d ranged from 14% to 18%. SV5d_3w showed small variation, probably due to a low mortality during this period.

Table 3 shows variance components as a proportion of the phenotypic variance of litter size at different stages. Proportion of variance due to sow genetic effect ranged from 0.081 to 0.111 in Landrace and from 0.065 to 0.106 in Yorkshire. The highest proportion is observed for N5d and N3w, the lowest for TNB, and NBA is in the middle of the range in both populations. The proportion of the variance component due to sire genetic effect ranged from 0.030 to 0.059 in

Landrace and from 0.024 to 0.034 in Yorkshire. The proportion of the variance component due to the sire genetic effect was higher for N5d and N3w than for NBT and NBA in Landrace, but not in Yorkshire.

Table 2. Mean and coefficient of variation (CV) for total number of piglets born (TNB), born alive (NBA), litter size at 5 days (N5d), at 3 weeks (N3w), survival rate at birth (SVb), from birth to 5 days (SVb_5d) and from 5 days to 3 weeks (SV5d_3w)

Traits	Landrace			Yorkshire		
	Lit. No.	Mean	CV %	Lit. No.	Mean	CV %
TNB	5178	14.23	25.44	3938	13.01	26.13
NBA	5178	11.61	27.13	3938	11.49	26.89
N5d	5178	10.06	30.22	3938	10.03	29.21
N3w	5178	9.76	31.25	3938	9.59	30.34
SVb	5178	82.72	17.78	3938	89.15	14.04
SVb_5d	5165	87.58	16.16	3918	88.31	16.16
SV5d_3w	5165	97.00	7.70	3917	95.74	8.91

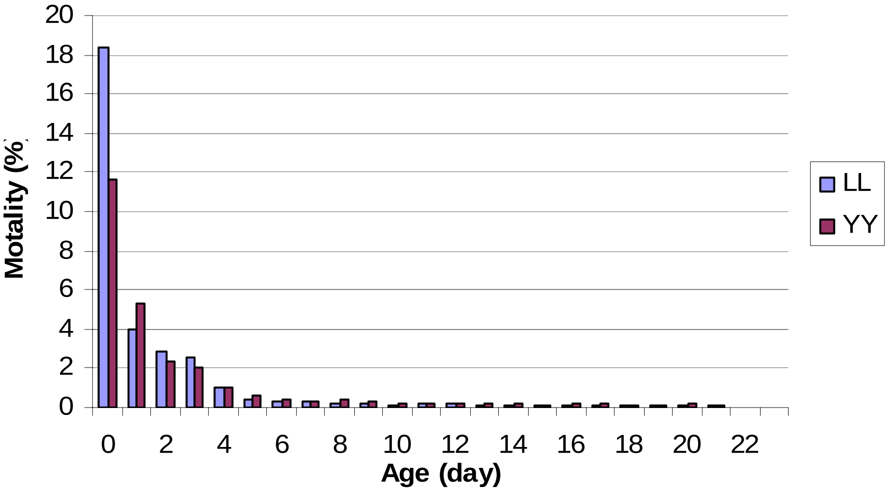

Figure 1. Mortality in relation to age of piglets in Danish Landrace (LL) and Yorkshire (YY)

Table 3. Phenotypic variance (Vp), proportions of sow variance (h^2_{sow}) and service-sire variance (h^2_{sire}) for litter size

Traits	Landrace			Yorkshire		
	Vp	h^2_{sow}	h^2_{sire}	Vp	h^2_{sow}	h^2_{sire}
TNB	11.74	0.081**	0.030**	10.64	0.065**	0.034**
NBA	9.49	0.096**	0.037**	8.85	0.080**	0.025**
N5d	8.78	0.110**	0.059**	7.98	0.106**	0.024**
N3w	8.76	0.111**	0.056**	7.95	0.105**	0.029**

**: Significant at p<0.01.

The correlations between litter sizes at different stages are shown in Table 4. Phenotypic correlation between TNB and N3w was 0.512 for Landrace and 0.592 for Yorkshire, while the correlation between N5d and N3w was 0.972 and 0.958 for Landrace and Yorkshire, respectively. Genetic correlations were estimated from the sow components. Genetic correlations between TNB and N3w were 0.39 in Landrace and 0.72 in Yorkshire. Genetic correlation between N5d and N3w was close to one (0.99) in both populations.

Table 4. Genetic correlation (based on sow genetic component, above the diagonal) and phenotypic correlation (below the diagonal) between litter sizes at different age stages.

Landrace					Yorkshire				
	TNB	NBA	N5d	N3w		TNB	NBA	N5d	N3w
TNB		0.67**	0.43**	0.39**	TNB		0.83**	0.76**	0.72**
NBA	0.741**		0.81**	0.75**	NBA	0.827**		0.93**	0.91**
N5d	0.546**	0.830**		0.99**	N5d	0.644**	0.814**		0.99**
N3w	0.512**	0.797**	0.972**		N3w	0.592**	0.764**	0.958**	

**: Significant at $p<0.01$.

Approximate results for survival are shown in Table 5. The proportion of sow genetic variance for SVb was significantly different from zero in both populations and the estimates in Landrace were twice as high as in Yorkshire. The variance component due to the service-sire was small but statistically significantly different from zero for SVb and SVb_5d in Landrace, and for SVb_5d in Yorkshire. Again the proportions were higher in Landrace than in Yorkshire. In the two populations, the variance components due to sow and sire genetic effects for SV5d_3w were close to zero.

Table 5. Phenotypic variance (Vp), proportions of sow variance (h^2_{sow}) and service-sire variance (h^2_{sire}) for survival rate in litter level.

Traits	Landrace			Yorkshire		
	Vp	h^2_{sow}	h^2_{sire}	Vp	h^2_{sow}	h^2_{sire}
SVb	210.68	0.127**	0.027**	155.01	0.073**	0.002
SVb_5d	196.23	0.127**	0.038**	192.45	0.043*	0.013*
SV5d_3w	54.99	0.016	0.003	71.71	0.009	0.004

*: Significant at $p<0.05$. **: Significant at $p<0.01$.

As shown in Table 6, phenotypic correlations of TNB with SVb and SVb_5d ranged from –0.205 to –0.273, but the phenotypic correlation with SV5d_3w was only about –0.08. In Landrace, the approximated estimates of genetic correlations between TNB and the three survival rates were all negative. Only the estimate between TNB and SVb_5d was significantly different from zero. In Yorkshire TNB showed a weak negative genetic correlation with SVb while it showed a weak positive correlation with SVb_5d and with SV5d_3w. However these estimates were not significantly different from zero. It was interesting that SVb showed a weak positive genetic correlation with SVb_5d but a strong positive genetic correlation with SV5d_3w in both populations.

Table 6. Genetic correlations (based on sow genetic component, above the diagonal), and phenotypic correlations (below the diagonal) between total number of piglets born and survival rate and between survival rates at different periods.

Landrace					Yorkshire				
	TNB	SVb	SVb_5d	SV5d_3w		TNB	SVb	SVb_5d	SV5d_3w
TNB		-0.178	-0.335*	-0.351	TNB		-0.149	0.169	0.178
SVb	-0.273**		0.194	0.703**	SVb	-0.258**		0.104	0.812**
SVb_5d	-0.247**	0.125**		0.668*	SVb_5d	-0.205**	0.043**		0.305
SV5d_3w	-0.081**	0.073**	0.130**		SV5d_3w	-0.076**	0.068**	0.115**	

*: Significant at $p<0.05$. **: Significant at $p<0.01$.

Discussion

Litter size, prenatal and pre-weaning mortality in Danish Landrace and Danish Yorkshire

Selection for total number of piglets born (TNB) since 1992 has led to a marked increase in this trait and an increase in mortality in Danish Landrace and Yorkshire. Despite the high mortality, litter size at weaning was high in both Danish Landrace and Danish Yorkshire. Landrace showed larger TNB but lower prenatal survival rate than Yorkshire. In contrast, Swedish results (Tummaruk et al., 2000) showed that TNB was lower and perinatal survival rate was higher in Swedish Landrace than in Swedish Yorkshire.

Heritability for litter size

Estimates of heritability for litter size reported in this study were consistent with those in the literature. As reviewed by Haley et al. (1988), most estimates of heritability for litter size are around 0.1. The variance due to sires as a proportion of the phenotypic variance ranged from 0.024 to 0.034 in Yorkshire and from 0.030 to 0.059 in Landrace. Theses estimates were consistent with reports in previous studies (Strang, 1970; Knap, 1986; Mabry et al., 1988; See et al., 1993; Woodward et al. 1993; Van der Lende et al., 1999; Hamann et al., 2004). This contribution could be due to genetic difference in semen quality and/or due to differences in survival between offspring genotypes. It is difficult to disentangle these two components.

Heritability for survival

Previous studies indicate that estimates of heritability for pre-weaning mortality or survival rate are low, with an average 0.05 (at the level of the litter, as a maternal trait). Estimates for prenatal survival are somewhat higher, with an average 0.15, as reviewed by Rothschild and Bidanel (1998). However there is rather large variation between estimates from different studies. For example, Lambertson and Johnson (1984) reported an estimate of heritability for pre-weaning survival of 0.03, while Ferguson et al. (1985) reported a value of 0.14 in Yorkshire and 0.18 in Duroc. Our preliminary analysis indicated that heritabilities (based on the sow component) for SVb and SVb_5d in Landrace were higher than those in Yorkshire. In addition heritability for SV5d_3w was close to zero in both Danish Landrace and Yorkshire, probably due to very low mortality during this period in the two populations.

The estimated proportions of the variation due to service-sire for survival rates were low (ranged from 0.002 to 0.038), but statistically significantly different from zero for SVb and SVb_5d in Landrace, and for SVb_5d in Yorkshire. Take variance of sire as 1/4 additive genetic variance into consideration, these estimates corresponded to the contribution of direct additive genetic effect in litter level being 0.108, 0.151 and 0.053 for SVb and SVb_5d in Landrace and for SVb_5d in Yorkshire, which were agreeable with the estimates reported by Van Arendonk et al. (1996). These results, if confirmed in a more thorough study, could indicate that direct additive genetic effects on survival are important in the two populations.

Genetic correlations among litter sizes and survival rates

It is usually accepted that genetic correlation between litter sizes at different time points is high due to the part-whole relationship. However, in the present study, the genetic correlation between TNB and N3w was 0.72 in Yorkshire while only 0.39 in Landrace. On the other hand, the genetic correlation between N5d and N3w was close to one (0.99).

High genetic correlations (about 0.5) between TNB and the number of piglets dead have been reported in previous studies (Lobke et al., 1983; Robinson and Quinton, 2002), but genetic correlation between TNB and survival rate seems weak. In the present study, the approximated estimates of genetic correlation between TNB and survival rates ranged from -0.178 to -0.351 in Danish Landrace and from -0.149 to 0.179 in Danish Yorkshire. Only the estimate between TNB and SVb_5d in Landrace was significantly different from zero. Similarly, Lund et al. (2002) showed a weak negative maternal genetic correlation between TNB and perinatal and between TNB and pre-weaning survival rate in Finnish Landrace (-0.16 and -0.39) and Finnish Yorkshire (-0.14 and -0.01).

Although the negative genetic correlation between TNB and survival rates is weak, long term's selection for NTB without considering survival rate would lead to a decrease in survivability of piglets. On the other hand, since the unfavourable genetic correlation was small, genetic improvement on TNB and survival rate simultaneously would be available.

Estimation of genetic parameters for survival rates

Genetic parameters for survival rates are often estimated by treating them as Gaussian traits. However the distribution of survival rate is typically far from symmetric. In general, the distribution is skewed with a large proportion of litters showing 100% survival rate. More appealing models for the analysis of mortality could be based on treating the piglet survival as a binary trait. Thus, genetic parameters for piglet survival can be estimated using a liability threshold model. Another possible approach is to estimate survival rate of the litter by fitting zero-inflated-Poisson models (Lambert, 1992).

Genetic improvement of litter size at weaning

Because of the difficulties to evaluate breeding values for N3w due to cross-fostering, genetic improvement on N3w by direct selection on this trait is not feasible. Therefore genetic improvement of litter size at weaning has focused on selection for TNB. However, the genetic correlation between TNB and N3w is not large enough to get large correlated response for N3w by selection on TNB. In addition the negative genetic correlation between TNB and survival rate (especially in Danish Landrace) implies that selection for TNB alone would lead to an increase in mortality. This has been observed over the last several years in the Danish pig breeding program.

Based on the estimated variance components and genetic correlations between litter sizes at different ages, relative to direct selection for N3w, the efficiency of genetic improvement of N3w by individual selection on sow for TNB is only 33% in Landrace and 57% in Yorkshire. Selection on the sow for NBA is 70% and 79% as efficient as direct selection for N3w. When selection is based on N5d, the efficiency is increased to 99%.

Results from a pilot study (not shown) involving cross-fostering data showed that the nursing sow had a small effect on survival rate during the first five days of age. This implies that breeding values for N5d can be well estimated even ignoring the status of the sow. Therefore selection based on N5d may be a good alternative to selection based on TNB for genetic improvement of N3w.

Another alternative is to select on an index including TNB and either survival rate to 5 days, or to weaning. If the nursing sow has a large effect on survival of the litter, evaluation of survival rate should be based on the status of the piglets remaining in their own litters, in order to avoid effects of cross-fostering on inferences about breeding values.

Acknowledgments

This study was supported by The Danish National Committee for Pig Production.

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