Genetic parameters for maternal behaviour traits in sows

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Abstract

Data from 32 nucleus and multiplier herds in Germany was used to estimate variance components and breeding values for five maternal behaviour traits in sows. The estimation was performed univariately using an animal threshold model. About 31,000 farrowings recorded from December 2003 until July 2005 were included. The heritability coefficients were 0.07 (0.06) for group behaviour, 0.06 (0.03) for attitude to people, 0.05 (0.01) for maternal ability, 0.03 (0.01) for crushing of piglets and 0.02 (0.02) for savaging of piglets. Additionally, genetic correlations between the behaviour traits and between the behaviour traits and litter size, respectively, were estimated multivariately by REML with a linear model. Low heritability and weak genetic correlation to litter size at birth indicate that it may be difficult to genetically improve the maternal behaviour, and that selection for better mothering ability is not necessarily accompanied by reduced litter size at birth.

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1. Introduction

Over the last years there has been an increase in litter size at birth and at weaning, whereas the survival rate of piglets has not been improved (Grandinson et al., 2003). For example, in Schleswig-Holstein, the northern part of Germany, piglet losses amount to 15.5% until weaning (LK and S.-H., 2005). Breeding against piglet mortality (survival rate) directly may be difficult because of several reasons (Grandinson, 2005). Survival rate shows a low heritability (Grandinson et al., 2002; Hellbrügge, 2007) and is affected by several environmental factors, and it is very difficult to consider the effect of crossfostering correctly. Moreover, survival rate is affected by both maternal genetic factors as well as direct genetic effects and negative genetic correlations between direct and maternal effects have been reported for survival in pigs (Van Arendonk et al., 1996; Lund et al., 2002).

An alternative strategy may be to breed for the sow’s maternal abilities (Grandinson et al., 2003), since a good maternal behaviour of the sow contributes to the piglet’s welfare and survival rate and consequently affects the economically important trait litter size at weaning. Recent studies indicate that some of the variation in piglet mortality between sows may be explained by individual differences in maternal ability (Wechsler and Hegglin, 1997; Spinka et al., 2000; Andersen et al., 2005).

Finding appropriate traits to describe maternal skills may not be easy. Various authors defined several different
traits to describe the mothering abilities of sows in different studies and the judgement of sows’ maternal behaviour was done either by questionnaire or by behavioural tests (Henne 1996; Knap and Merks, 1987; Grandinson et al., 2002, 2003; Lovendahl et al., 2005; Vangen et al., 2005; Hellbrügge et al., 2006). Traits from recent studies characterising the maternal behaviour were, for example, the sow’s reaction being separated from its litter and the sow’s reaction to a piglet’s distress call (Grandinson et al., 2003; Lovendahl et al., 2005; Hellbrügge et al., 2006). The first trait describes the sow’s response towards her piglets being in difficulties and additionally the sow’s behaviour towards the person that handles the piglets. The second trait was used to test the sow’s reaction to the distress call from a piglet, as if it is being crushed under the sow, and may reflect the sow’s responsiveness toward her piglets. Spinka et al. (2000) stated two aspects of the sow’s behaviour influencing the probability of crushing, first, the sow’s general restlessness and her lying-down behaviour, and secondly, the sow’s individual reactivity to a screaming piglet. Grandinson et al. (2003) showed that alertness to piglet screams is genetically related to the survival of piglets. Some further investigated traits were crushing of piglets, savaging of piglets, aggression towards the stockperson and nursing behaviour (Henne 1996; Knap and Merks, 1987; Grandinson et al., 2002, 2003; Vangen et al., 2005; Hellbrügge et al., 2006).

Before selection can be used as a tool to improve maternal behaviour and thereby improve piglet survival, reliable estimates of genetic parameters including genetic correlations to other important traits are necessary. Estimates of the genetic variation of maternal ability in sows are scarce in the literature and the available heritabilities are generally at low level (Henne 1996; Knap and Merks, 1987; Grandinson et al., 2002, 2003; Lovendahl et al., 2005; Vangen et al., 2005, Hellbrügge et al., 2006). The long term aim of selection for a better maternal behaviour is to reduce the piglet losses until weaning or in other words to increase the piglet survival rate until weaning. This results in an increased economic gain and additionally in an improved animal welfare.

The aims of the present study were first to define five behaviour traits which characterise the mothering abilities of sows and subsequently to obtain estimates of variance components and breeding values for these traits in order to assess the suitability of the traits as selection criteria. Finally, genetic correlations between litter size at birth and the behaviour traits were estimated in order to test if selection for improved maternal behaviour is associated with number of piglets born alive.

Table 1
Definitions of the five behaviour traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Description of trait</th>
<th>Scale</th>
<th>Legend</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Group behaviour</td>
<td>Biting, bullying, chasing away from feeder, mounting</td>
<td>1–3</td>
<td>1: submissive/fearful; avoids feeding place 2: normal/tolerant 3: dominant/ aggressive</td>
</tr>
<tr>
<td>2. Attitude to people</td>
<td>In farrowing crate during piglet processing</td>
<td>1–3</td>
<td>1: fearful/jumpy 2: normal/tolerant 3: aggressive/biting</td>
</tr>
</tbody>
</table>
| 3. Maternal ability | • Behaviour during farrowing  
• Behaviour during lying down  
• Nursing behaviour  
• Reaction to piglet’s screams  
• Crushed piglets | 1–5   | 1:  
• very calm behaviour during farrowing  
• very careful behaviour during lying down, spending a lot of time looking at the piglets  
• lying in lateral position during nursing  
• strong reaction (standing up) towards screaming piglets  
• no crushed piglets  
...  
5:  
• very restless during farrowing  
• abrupt lying down without looking at the piglets  
• often standing and sitting position  
• no reaction towards screaming piglets  
• repeated crushed piglets (above-average) |
| 4. Crushing of piglets | During lactation | 1–2   | 1: no piglet crushed 2: at least one crushed piglet |
| 5. Savaging of piglets | Shortly after farrowing | 1–2   | 1: normal/tolerant 2: aggressive/biting |
2. Material and methods

2.1. Data set

Data were available of approximately 31,000 farrowings recorded between December 2003 and July 2005. Five behaviour traits in sows were defined (Table 1) and recorded routinely by farm staff at 32 nucleus and multiplier farms in Germany. About 40% of the sows had one observation, about 30% had two, about 16% had three and about 13% had four records. The sows came from three genetic lines (20% PIC Large White, 7% PIC Landrace and 73% from their crosses). The sows were housed in farrowing crates during farrowing and lactation. For the period of gestation most sows were kept in crates. Only few farms had group housing throughout pregnancy. Pedigree information contains sires and dams three generations back, in total about 22,000 animals appeared in the pedigree file.

Data editing left unequal numbers of records per trait (Table 2). In total there are 15,369 sows providing information, daughters of 465 sires, that is 33 daughters per sire on average. Descriptive statistics for the behaviour traits are given in Table 2.

2.2. Traits and recording procedures

The objective was to obtain a large field data set (on 32 nucleus and multiplier farms). Vangen et al. (2005) showed that collecting data on maternal behaviour with questionnaires seems to work in a large scale under field conditions. Hence, farms got questionnaires and recorded data directly in the barns on the farrowing sow cards. At each farm up to 3 people, who were trained and experienced workers, recorded the data.

The defined behaviour traits were group behaviour, attitude to people, maternal ability, crushing of piglets and savaging of piglets (Table 1). Group behaviour was assessed during 3 days after mixing the sow into the group. On a scale with three marks it was judged if the sow behaved submissive and fearful (“1”), normal (“2”) or dominant and aggressive (“3”) towards the other sows in the group. Since only one third of the farms had group housing for the period of gestation, less data was available for this trait. In farms with group housing during gestation, the mixing of the sows into groups used to happen after successful pregnancy control from the 30th day of gestation. Attitude to people was evaluated 3 to 5 days after farrowing during piglet handling. An anxious and jumpy sow got a “1”, a normal and tolerant sow a “2” and a “3” characterised an aggressive and biting sow. The trait maternal ability was evaluated 3 to 5 days after farrowing and combined several aspects: the sow’s behaviour during farrowing, the sow’s behaviour during lying down in the farrowing pen (considerateness to the piglets), nursing behaviour (position of the sow during nursing), reaction to piglets’ screams and crushing of piglets during that time. Maternal ability was scored on a scale from one to five, where from one to five the trait becomes worse. Crushing was scored before weaning at around 21 days. Here a “1” denoted that no piglets were crushed and a “2” that at least one piglet was crushed in the respective litter. The trait savaging of piglets, i.e. piglet-directed biting around the time of farrowing, was recorded in the first 24 h after farrowing as a savaging sow occurs predominantly during farrowing and sometimes in the first 24 h afterwards. A normal behaviour of the sow got a “1” and a “2” described an aggressive and biting sow.

For statistical analysis records were excluded which did not supply information about the respective traits. Fixed-effect classes with <100 observations and with no variation were eliminated, the latter to avoid the extreme category problem (all observations of the respective effect stage fall into the same category of response) which can cause biased results, as there is no information in the data to estimate these fixed effects (Sorensen and Gianola, 2002).

2.3. Statistical models

2.3.1. Systematic effects influencing maternal behaviour

The significance of systematic environmental effects on the behaviour traits was investigated in a fixed-effect analysis, ignoring random permanent environmental and genetic effects. The following effects were tested for significance: parity, breed and the combined farm season effect, the latter one representing the environmental effect of the farm in different time periods. Each season class comprised 4 months. The analysis of the fixed effects was done with the SAS-procedure GENMOD (SAS Institute Inc., 2000), using a binomial
(binary traits) and a multinomial distribution of the scores (traits with more than two categories), respectively, and a probit link function (binary traits) and a cumulated probit link function (multiple ordered threshold traits).

2.3.2. Threshold models

Variance components for the behaviour traits were estimated univariately. For the binary traits (savaging and crushing) a Bayesian threshold liability animal model was used and for the remaining traits with multiple ordered categories (attitude to people, group behaviour, maternal behaviour) a Bayesian multiple ordered threshold animal model was applied. Thereby information on a particular trait at different parities was modelled as repeated observations of the same trait. The option to include different parities in a multiple-trait model was not pursued due to insufficient data. In the threshold model an unobservable normally distributed variable (liability) is assumed for each observation. When the liability exceeds a certain threshold, the outcome of the behaviour falls into the next category (Falconer and Mackay, 1996).

The following repeatability model was applied for the analysis of the traits maternal ability, crushing of piglets and savaging of piglets:

$$\lambda = X\beta + Zu + Wpe + e,$$

where $$\lambda$$ is the vector with the unobservable liability of the respective observation, $$\beta$$ is the vector of the fixed effects comprising the combined farm season effect, the parity effect, and the breed effect. Vector $$u$$ contains the random correlated animal effects with $$\text{cov}(u) = A\sigma^2_u$$, $$A$$ being the numerator relationship matrix and $$\sigma^2_u$$ is the additive genetic variance. Vector $$pe$$ contains the random permanent environmental effects with $$\text{cov}(pe) = I\sigma^2_{pe}$$, $$I$$ being the identity matrix and $$\sigma^2_{pe}$$ is the permanent environmental variance. Vector $$e$$ contains the residuals. In comparison to the traits maternal ability, crushing of piglets and savaging of piglets, the model applied for the analysis of the traits group behaviour and attitude to people excluded the effect of breed (group behaviour and attitude to people) and parity (group behaviour) due to lack of statistical significance.

The Bayesian posterior distributions of the permanent environmental variance and the additive genetic variance of the liabilities for the different traits were determined through Gibbs sampling as implemented in the program LMMG_MTH (Reinsch 1996, extended version). The liability values were created by data augmentation, as described by Sorensen et al. (1994), drawing random variables from truncated normal distributions, which are conditional upon the other fixed and random effects in the model.

The Gibbs sampler was run in a single, long-chain scheme. The sampler ran 300,000 (crushing and savaging of piglets) and 1 million rounds (group behaviour, attitude to people, maternal ability), respectively. Convergence was determined by visual inspection. The results of the first 120,000 (crushing and savaging of piglets) and 300,000 (group behaviour, attitude to people and maternal ability) iterations, respectively, were discarded (burn-in), and the remaining iterations were used to estimate the variance components. The posterior mean of the additive genetic variance and the permanent environmental variance were estimated as the mean of all iteration estimates, following Sorensen et al. (1994). The effective sample size was estimated using time series methods as described by Sorensen et al. (1994) applying the SAS-procedure AUTOREG (SAS Institute Inc., 2000). Because for the traits with multiple categories also thresholds were sampled, the autocorrelations between samples were greater for these traits than for the binary traits. Therefore, a greater number of samples were chosen for these traits. The effective sample size was >350 for the variance components for all traits.

2.3.3. Linear model for correlated trait litter size at birth

Genetic correlations between the behaviour traits and litter size at birth were estimated multivariate by REML with a linear model to test if selection for better maternal behaviour is associated with number of piglets born alive. The model applied to the trait number of piglets born alive corresponded to the model used for the behaviour traits. Again a repeatability model was used for all behaviour traits and for litter size as well. Roche and Kennedy (1995) recommended to consider litter size at different parities as different

<table>
<thead>
<tr>
<th>Breed</th>
<th>Crushing of piglets</th>
<th>Savaging of piglets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landrace</td>
<td>27.7 (7.3)</td>
<td>3.8 (18.1)</td>
</tr>
<tr>
<td>Large White</td>
<td>26.5 (7.1)</td>
<td>2.6 (18.4)</td>
</tr>
<tr>
<td>Crossbred</td>
<td>31.0 (3.6)</td>
<td>4.1 (8.2)</td>
</tr>
<tr>
<td>Parity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>24.0 (5.5)</td>
<td>4.4 (12.3)</td>
</tr>
<tr>
<td>2</td>
<td>24.0 (5.6)</td>
<td>3.0 (13.3)</td>
</tr>
<tr>
<td>3</td>
<td>28.5 (5.6)</td>
<td>3.2 (13.3)</td>
</tr>
<tr>
<td>4</td>
<td>29.7 (6.0)</td>
<td>3.2 (14.0)</td>
</tr>
<tr>
<td>5</td>
<td>31.0 (6.5)</td>
<td>3.5 (14.5)</td>
</tr>
<tr>
<td>From 6</td>
<td>33.2 (5.4)</td>
<td>3.6 (12.9)</td>
</tr>
</tbody>
</table>
characteristics and consequently to apply a multiple-trait model, but found genetic correlations between direct effects of different parities to be sufficiently large to use a repeatability model for improving litter size across all parities. Because of an unfavourable data structure, the traits group behaviour and attitude to people were not included in the estimation of genetic correlations. For the estimation of the genetic correlations the VCE 4 package was used (Neumaier and Groeneveld, 1998).

2.3.4. Estimation of breeding values

For the estimation of BLUP breeding values the same Gibbs sampling algorithm was used a second time with the variance components kept fixed at their estimated mean values. The posterior mean of the random animal effects provided estimates of breeding values on the liability scale. The reliabilities for the breeding values \( R_i \) were estimated by

\[
R_i = 1 - \frac{\text{PEV}_i}{\sigma^2_a},
\]

where \( \text{PEV}_i \) is the prediction error variance of animal \( i \), which was approximated by the variance of the estimated iteration animal effects, and \( \sigma^2_a \) is the posterior mean of the additive genetic variance. The breeding values on the underlying liability scale were transformed to the phenotypic scale using:

\[
p_{ij} = \Phi\left(\mu_i + \text{EBV}_{ij}\right)*n_{\text{cat}} - 1,
\]

where \( p_{ij} \) corresponds to the expected category of trait \( i \) in animal \( j \), \( \Phi \) is the cumulative probability function of the standard normal distribution, \( \mu_i \) is the probit function corresponding to the mean liability of trait \( i \) and \( \text{EBV}_{ij} \) is the breeding value estimated on the liability scale for trait \( i \) and animal \( j \) and \( n_{\text{cat}} \) is the number of possible categories regarding trait \( i \).

3. Results

3.1. Fixed effects influencing maternal behaviour

Parity had an effect on all investigated traits, except for group behaviour. Problems with savaging were observed more frequently in first parity sows (Table 3). The least amount of crushing was in young sows, and crushing increased in later parities (Table 3).

The breed affected maternal ability significantly but seemed to affect also crushing and savaging \((p < 0.06)\). Therefore, the breed effect was included in the models for these three traits. The cross (Large White* PIC Landrace) showed a higher incidence for crushing and savaging (Table 3) and a worse maternal ability than the two purebreds.

The effect of the farm season was significant for all behaviour traits. As presented in Table 4 considerable differences exist in the incidence of savaging sows among the different farms in different time periods (seasons) (LSM range from 0% up to 48%).

<table>
<thead>
<tr>
<th>Trait</th>
<th>( \sigma^2_a ) (Std)</th>
<th>( \sigma^2_{pe} ) (Std)</th>
<th>( h^2 ) (Std)</th>
<th>( t ) (Std)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Group behaviour</td>
<td>0.10 (0.10)</td>
<td>0.25 (0.21)</td>
<td>0.07 (0.06)</td>
<td>0.24 (0.12)</td>
</tr>
<tr>
<td>2. Attitude to people</td>
<td>0.07 (0.03)</td>
<td>0.15 (0.06)</td>
<td>0.06 (0.03)</td>
<td>0.18 (0.04)</td>
</tr>
<tr>
<td>3. Maternal ability</td>
<td>0.05 (0.01)</td>
<td>0.11 (0.02)</td>
<td>0.05 (0.01)</td>
<td>0.14 (0.01)</td>
</tr>
<tr>
<td>4. Crushing of piglets</td>
<td>0.03 (0.01)</td>
<td>0.05 (0.03)</td>
<td>0.03 (0.01)</td>
<td>0.07 (0.02)</td>
</tr>
<tr>
<td>5. Savaging of piglets</td>
<td>0.04 (0.04)</td>
<td>0.68 (0.20)</td>
<td>0.02 (0.02)</td>
<td>0.41 (0.07)</td>
</tr>
</tbody>
</table>

\( \sigma^2_e \) was set to 1.
Heritability for the number of liveborn piglets was estimated to be 0.07. Savaging and crushing of piglets were also studied, with heritabilities of 0.22 and 0.34, respectively. A strong permanent environmental effect was observed, as indicated by the heritability estimates. Maternal ability had a weak negative correlation with savaging, suggesting an unfavourable relationship. The heritability for savaging was lower than for crushing, indicating less genetic influence.

### 3.2. Variance components

Table 5 shows the estimated heritabilities and repeatabilities. Posterior distributions of $h^2$ for the behaviour traits except group behaviour and attitude to people are shown in Fig. 1. This shows almost symmetric distributions for the behaviour traits, except for the posterior distribution of savaging, which tended to be skewed to the left as the estimate is close to zero. The heritabilities, ranging from 0.02 up to 0.07 for the five behaviour traits, are low especially for crushing and savaging. The group behaviour, attitude to people and maternal behaviour showed slightly higher heritabilities ($h^2 = 0.05–0.07$) compared to crushing and savaging of piglets. The repeatabilities range from 0.07 up to 0.41 (Table 5). Especially savaging shows a high repeatability because of a strong permanent environmental effect, which includes in our study also dominance and epistasis.

### 3.3. Genetic correlations

The estimated genetic correlations between the maternal behaviour traits and the number of piglets born alive are shown in Table 6. The heritability for the litter size was 0.07 (0.00). The correlation of maternal ability with litter size is around zero. The correlation between savaging and litter size is favourable ($r_g = -0.34$), i.e. sows with more piglets born alive tend to be less aggressive to their offspring. The correlation between crushing and litter size is positive ($r_g = 0.30$), meaning that the probability to crush at least one piglet increases with larger litter size. Concerning the correlations among the behaviour traits the estimate between maternal ability and crushing is strong with 0.78, indicating that a poor maternal ability is associated with more problems in terms of crushing. The correlation between maternal ability and savaging is at a medium level with 0.43, indicating that a poor maternal ability is associated with more problems in terms of savaging. Between crushing and savaging the estimated weak negative correlation indicates an unfavourable relationship.

### 4. Discussion

#### 4.1. Fixed effects influencing maternal behaviour

Looking at the differences in the incidence of savaging sows among the different farms in different time periods (seasons) in Table 4 it may be a concern to find out the environmental factors which control the fact that in some farms considerable problems with savaging of piglets occur only temporarily (Henne, 1996). Problems with savaging were observed most frequently in first parity sows. Possible reasons for this phenomenon are excessive demand and lack of experience of the gilt, since being put into the farrowing pen, the change of food and climate, and furthermore the parturition itself are new experiences for the young sow. Gilts savage their piglets more frequently compared to sows of later parities, because piglets are unknown objects to the young sow (Vangen et al., 2005; Henne, 1996; Harris et al., 2003). Crushing increased in upper parities. Based on the definition of the trait crushing from the present study (a zero means no crushed piglets and a one means, at least one piglet was crushed in the respective litter) a possible explanation is the increase in litter size in higher parities. Additionally, in higher parities the sow’s body weight and leg problems increase, and litters become more uneven with respect to the growth of the piglets. This might increase the probability to crush at least one piglet. For this reason it may be more appropriate to record the exact number of crushed piglets per litter. Grandinson et al. (2003) and Vangen et al. (2005) found that first parity sows reacted more strongly to the sound of a screaming piglet which may result in fewer crushed piglets and Hellbrügge (2007) observed a trend that with increasing parity the fraction of crushed piglets increases.

In the present study cross bred sows showed worse maternal behaviour in comparison to the two purebreds. Breed effects in maternal behaviour were previously reported by Vangen et al. (2005), where Yorkshire sows were less aggressive towards piglets and reacted less when their piglets were handled than Finnish Landrace. Knap and Merks (1987) showed that Duroc sows were more aggressive towards piglets than Landrace sows and that crossbreds were more aggressive than purebred Landrace and Duroc. However, it was in this and other studies difficult to make an appropriate comparison of...
two maternal breeds because very few farms hold purebred sows of different breeds in their herd which is necessary in order to separate the herd from the breed effect (Vangen et al., 2005).

4.2. Variance components

Because of the low heritabilities for the five behaviour traits, the potential for progress by selection seems to be limited, not exceeding the progress possible for litter size. As the data are from multiple farms and several people were involved in the management and judgement of the sows, the heritabilities are expected to be of lower magnitude than from other studies (e.g. Hellbrügge et al., 2006).

A general problem in comparing results from literature is that different traits are defined to describe the mothering abilities of the sow. Additionally, these traits are recorded and analysed in different ways. Thus, drawing conclusions from results of other studies must be done with care during interpretation of the own outcomes.

In agreement with our results Hellbrügge et al. (2006) estimated a low heritability of 0.03 for the trait crushing based on 1500 litters and applying a threshold model. Hellbrügge et al. (2006) treated each piglet (crushed or not) as a repeated observation of the sow and subsequently estimated heritabilities that are comparable to our results. Grandinson et al. (2002) calculated a slightly higher heritability of 0.06 for the trait crushing as well as a binary trait of the piglet and estimated with a threshold model. As a result of preliminary studies the authors assumed that crushing is exclusively a maternal trait, under no influence of the piglet’s own genes.

Concerning the trait savaging, Vangen et al. (2005) estimated heritabilities of 0.00 to 0.04 for the trait aggressive behaviour towards piglets at farrowing. However, Vangen’s trait was recorded on a scale from 1 to 7, and estimation was done with a linear model. In general, heritabilities estimated on the observed scale are expected to be lower than heritabilities on the assumed underlying scale estimated with a threshold model (Dempster and Lerner, 1950). Henne (1996) got a considerably higher heritability estimate of 0.17 using a threshold model for savaging of piglets in primiparous sows. In contrast to the conclusion of Henne (1996) the results of the present study indicate that breeding against savaging of piglets is hampered by low heritability.

From the phenotypic distributions (Table 7) there seems to be little need for a genetic improvement with respect to the two traits group behaviour and attitude to people in the pig populations studied here, because very few observations on these traits fell into the categories 1 and 3, respectively, indicating that most sows behave normal and do not show aggression or fear in the group or towards the stockperson. But nevertheless we also estimated genetic parameters for these two traits group behaviour and attitude to people. Since the number of observations in the extreme categories was very small for group behaviour and attitude to people, the analysis was difficult for these two traits. Additionally, the ordinal scale assumed for these traits might not be appropriate. This makes it necessary to treat carefully the genetic parameters for attitude to people and group behaviour from the present study. Accordingly, the estimated heritabilities for group behaviour and attitude to people showed large standard errors. Using a finer scale probably would have been resulted in a less extreme phenotypic distribution. However, for traits, which are supposed to be recorded routinely on a large scale under field conditions, a very clear definition of the traits is required and a simple scale is favourable because many different people use to do the scoring and it is difficult to make sure that all observers do the scoring consistently.

Grandinson et al. (2003) used the traits avoidance of the stockperson (may reflect underlying fear) and aggression towards the stockperson which have similarities to our trait attitude to people. The authors got heritability estimates of 0.08 with a threshold model for both traits. According to this, it should be possible to select against aggression in order to make the sows easier for the farmer to handle and to select against fear in order to increase the welfare of both sows and their piglets. The trait attitude to people in the present study comprises both behaviour patterns fear and aggression, as attitude to people describes if a sow behaves anxious, normal or aggressive towards the farm staff. Lovendahl et al. (2005) studied the traits performed aggression and received aggression in sows at mixing. The group behaviour in the present study comprises performed aggression and received aggression in one trait, as group

<table>
<thead>
<tr>
<th>Phenotypic category</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group behaviour</td>
<td>2.6</td>
<td>96.1</td>
<td>1.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Attitude to people</td>
<td>1.9</td>
<td>96.5</td>
<td>1.5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Maternal ability</td>
<td>33.8</td>
<td>41.3</td>
<td>18.4</td>
<td>3.9</td>
<td>2.6</td>
</tr>
<tr>
<td>Crushing of piglets</td>
<td>68.4</td>
<td>31.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Savaging of piglets</td>
<td>95.0</td>
<td>5.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

* For descriptions of phenotypic category see Table 1.
Similarly, Hellbrügge et al. (2006) estimated a genetic piglets per litter and this trait is now recorded routinely. An alternative with larger litter size the probability to crush at least one between crushing and litter size was expected, because genetic correlation. The estimated positive correlation between number of piglets born alive and heritability estimates for single aspects of this trait out of literature are find estimates in literature to compare with. Some several aspects of maternal behaviour it is difficult to maternal ability is a complex trait which combines more possibilities for selection. Because the trait heritability of the trait maternal behaviour indicates more possibilities for selection. Because the trait maternal ability is a complex trait which combines several aspects of maternal behaviour it is difficult to find estimates in literature to compare with. Some heritability estimates for single aspects of this trait out of literature are \( h^2 = 0.07 \) for the trait “exposing her udder to the piglets at suckling” and \( h^2 = 0.06 \) for sow’s reaction to piglet scream (Grandinson et al., 2003; Vangen et al., 2005). But as already mentioned it is difficult to compare results from different studies not only because of varying definition of traits but also because different scaling of the traits and models used for analysing the data.

A large permanent environmental effect of the sow for the trait savaging makes a high repeatability which means that a sow which savaged her piglets once is likely to do so again in subsequent parities. Henne (1996) also found a high repeatability of about 0.32 for savaging. In agreement, Harris et al. (2003) found that sows that savaged as gilts were more likely to savage in their second parity compared to those that did not savage their first litter.

The heritability for the litter size was 0.07 and is in the range of estimates out of literature (e.g. Rohe and Kennedy, 1995).

### 4.3. Genetic correlations

The negative correlation between savaging and litter size from the present study suggests that sows with more piglets born alive tend to less likely to savage piglets. In contrast Henne (1996) found a small but unfavourable genetic correlation. The estimated positive correlation between crushing and litter size was expected, because with larger litter size the probability to crush at least one piglet is increased (definition of the trait). An alternative to this binomial trait is the exact number of crushed piglets per litter and this trait is now recorded routinely. Similarly, Hellbrügge et al. (2006) estimated a genetic correlation between number of piglets born alive and crushing of around 0.5, indicating that higher litter sizes are associated with more problems with respect to crushing.

The strong genetic correlation of 0.78 between maternal ability and crushing results from the definition of the characteristics since crushing is one included item within the trait maternal ability. The close correlation between maternal ability and savaging was expected because a negative grading in respect of savaging will implicate a negative judgement by the farmer of maternal ability. Between crushing and savaging the estimated weak negative correlation indicates an unfavourable relationship (but the standard error is high) insofar savaging sows tend to crush less piglets. However, this estimate could result from the fact that savaging sows also tend to have smaller litter sizes (\( r_{g} = -0.34 \) between savaging and litter size) and smaller litter sizes in turn implicate a lesser risk to crush at least one piglet. Again, it might be of interest to investigate the genetic correlation between savaging and the exact number of crushed piglets per litter.

### 4.4. Estimated breeding values

The estimated breeding values on the phenotypic scale give an idea of the scope for genetic improvement by selection. These breeding values correspond to the expected category of the respective trait. Figs. 2 and 3 illustrate the variation of estimated breeding values on the phenotypic scale. Sires’ EBVs for savaging vary only from 0.04 to 0.07 (this means an expected incidence regarding savaging of 4 to 7%). In contrast, the corresponding EBVs for crushing show more variation. The best sire’s breeding value was 0.25 and the worst sire’s EBV was 0.41 (this means an expected incidence regarding crushing of 25 to 41%), thus, providing more scope for selection compared to savaging. The EBVs for maternal ability show a difference of one categorical unit between the best and the worst sires, i.e. this trait does not supply much scope for selection either.

### 4.5. Selection of appropriate traits

The question which of the five investigated behaviour traits may be suitable for improving maternal ability by selection is important. Sows are faced with repeated social challenges through the continuous regrouping of animals at certain stages of the production (Andersen et al., 2005), thereby less aggressive behaviour may be beneficial to the welfare of group housed sows. A study from Lovendahl et al. (2005) indicated that less aggressive sows at
grouping tended to be stronger responding mothers. That is why the trait group behavior is suggested to be appropriate for improving the welfare of the sows and in addition the maternal ability. Studies concerning aggression after mixing unfamiliar pigs have shown that there is a great variability in the levels of aggression shown by individual pigs (Erhard and Mendl, 1997), thus, indicating scope for selection for a better group behavior.

The trait attitude to people differentiates between fear and aggression towards the farm staff. Stockperson directed aggression could arise from the increased maternal protectiveness after farrowing, from defensive aggression or from dominance aggression (Marchant Forde, 2002). In general, assertive behaviour of sows against unknown and therefore potentially dangerous factors, which may turn into aggressive behaviour when necessary, may be positive for piglet survival. As already mentioned the distribution of the traits group behavior and attitude to people in the present study raises the question of the need for a genetic improvement. Nevertheless, in case of future work on these traits, another definition should be considered. An alternative would be to separate the trait group behavior into the two binary traits fear and aggression towards other sows. Similarly, the trait attitude to people could be split into the two traits fear and aggression toward the farm staff. This would circumvent the necessity that the traits have to be ordinally scaled. The trait group behavior in the present study was observed during 3 days after grouping the sows. As McGlone (1986) and Messe and Ewbank (1973) said that most conflicts happen within the first hours after mixing the sows into new groups, it may be sufficient to judge the sows only in these first hours after grouping the animals to increase the variance of the trait.

The trait maternal ability from our study summarizes several aspects of maternal behaviour, this complicates a clear grading of the sows during data recording. It may be an alternative to work with the respective single traits, e.g. the sow’s carefulness at standing-to-lying as sow anti-crushing behaviour, the nursing behaviour or the reaction to piglets’ screams (Grandinson et al., 2003; Valros et al., 2003; Vangen et al., 2005; Hellbrügge et al., 2006). Furthermore, the high genetic correlation between maternal ability and crushing of piglets of about 0.8 indicates a low additional value of the trait maternal ability over crushing of piglets.

In the present study savaging occurred in 5% of the litters. Other studies found also 5% (Harris and Gonyou, 2003), 8–10% (Vangen et al., 2005) and 7–13% (Knap and Merks, 1987) savaging sows. In Grandinson et al. (2002) savaging causes 3.8% of total piglet deaths until 3 weeks of age. In contrast to savaging, maternal aggression directed towards the stockperson may represent a positive behavioural characteristic, in terms of potential benefits for piglet survival. The relationship between savaging and aggressive behaviour towards the stockperson may be interesting to ascertain (Marchant Forde, 2002). In our opinion the trait savaging of piglets can be recorded almost objectively although Harris and Gonyou (2003) noted that savaging is clearly a subjective measure that is very susceptible to both the stockperson’s degree of vigilance and his perception of the significance of this behaviour. Anyway, according to results from this study and from literature savaging seems to be lowly heritable (Table 5). Furthermore, since savaging is a trait with a low incidence at least in this study, improvement by selection will be limited. Knap and Merks (1987) raised the question, if savaging should be regarded as an exaggerated expression of extreme mothering abilities. Accordingly, Ahlström et al. (2002) observed that savaging gilts were significantly more restless and more responsive towards their piglets during farrowing compared to non-savaging gilts. As McGlone (1986) and Messe and Ewbank (1973) said that most conflicts happen within the first hours after mixing the sows into new groups, it may be sufficient to judge the sows only in these first hours after grouping the animals to increase the variance of the trait.
savagers. Savaging sows showed increased posture changing and spent more time investigating their piglets. The authors suggested that savaging may not necessarily reflect poor maternal ability, but may be related to the individual’s inability to cope with restrictive environments around farrowing. Jarvis et al. (2004) also found savaging gilts to be more active and responsive to piglets. Given this information it is still clear that breeding should not be for increased savaging.

Crushing causes a serious part of piglet deaths. A study with 80,000 piglets showed that about 5% of all piglets born alive die by means of crushing (Kunz and Ernst, 1987). Wechsler and Hegglin (1997) and Andersen et al. (2005) found that crushing as a cause of neonatal death in piglets is highly related to mothering style. The authors reported that in comparison to sows with at least two crushed piglets, sows that did not crush any piglets performed more nest building activity, responded sooner on piglet distress calls, initiated nose contacts sooner after presentation of distress calls, nosed more on the piglets during posture change, were more restless when the piglets were taken away and were socially more flexible in a grouping situation (Andersen et al., 2005). The trait crushing of piglets has the advantage of relatively easy and objective recording. Future studies will include number of crushed piglets per litter once but requires sufficient data to be available. Crushed piglets that were injured, since they were already underweight, diseased or weak at time of crushing due to low milk intake (starvation increases the risk for piglet crushing (Damm et al., 2005)), may not be assigned to the fraction of crushed ones as they were not crushed as a result of the dam’s disability. But this problem may be hard to solve during recording of crushing on a large scale.

5. Conclusion

Maternal behaviour of sows may be hard to change by selection because the traits are in general lowly heritable. Therefore the emphasis should be on the optimisation of the environment, and further investigations are needed to analyse the possible environmental factors which influence maternal behaviour. Including maternal behaviour in breeding programmes requires appropriate traits. These must be precisely defined, as objectively as possible, easy to record on a large scale and sufficiently genetically determined. From the five defined and analysed traits in the present study crushing seems to be the most promising trait for selection. Even though the estimated heritability was low, it shows a high incidence and is relatively easy to record objectively on a large scale.

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