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Genetics of the Interval from Weaning to Estrus in First-Litter Sows: Correlated Responses[1]

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ABSTRACT: The objective of this study was to evaluate relationships between rebreeding performance and growth performance (n = 3,777 gilts) and rebreeding performance and reproductive performance (n = 2,242 sows). Our data were from a selection experiment for shorter intervals from weaning to estrus after the first parity (IWE), involving Dutch Landrace pigs, in which a selection line and a control line without selection were maintained for eight generations. Relationships were evaluated before and after transforming IWE to normal interval (NI; IWE ≤ 7 d), prolonged interval (PI; IWE > 7 d), and incidence of a prolonged interval (INC). Heritabilities of NI, PI, and INC were .18, .17, and .27. Within-line phenotypic and genetic trends in growth and reproductive performance were not different from zero and did not diverge as a correlated response to the selection applied. Phenotypic correlations between IWE, NI, or PI and growth or reproductive performance were low and ranged from –.14 to .11. Genetic correlations were higher, and, for the majority of traits, the genetic correlations with NI and PI had a different sign. Phenotypic and genetic contrasts between sows with NI and sows with PI different from zero indicated that INC may increase as a correlated response to selection for reproductive performance. Analyses using untransformed IWE or data from populations selected for rebreeding performance may underestimate the correlated response in IWE due to selection on economically important traits.

Key Words: Reproductive Traits, Selection, Correlated Traits, Growth, Conformation, Pigs

Introduction

Intervals from weaning to estrus can be regarded as normal or prolonged. Variation in the interval from weaning to estrus is determined by variation in the incidence of prolonged intervals, duration of normal intervals, and duration of prolonged intervals (Ten Napel et al., 1995a). Genetic selection was effective for reducing the intervals from weaning to estrus. A shorter average interval was achieved by decreasing the incidence of prolonged intervals, rather than by changing the mean duration of normal or prolonged intervals (Ten Napel et al., 1995b). However, Ten Napel and Johnson (1997) concluded from analyses of field data that genetic selection for increased daily gain and reduced backfat may increase the liability for a prolonged interval.

Performance during lactation determines to a large extent whether a sow will have a normal return to estrus (King and Williams, 1984; Mullan and Williams, 1989; Ten Napel et al., 1995b). Severe losses of body weight and(or) backfat increase the interval to first estrus after weaning, especially in primiparous sows (Reese et al., 1982a,b; Brendemuhl et al., 1987, 1989).

The objectives of this study were to evaluate 1) the relationships between performance in the rearing period and reproductive performance as a first-litter sow and 2) rebreeding performance after weaning the first litter. We first studied phenotypic and genetic trends in rearing and breeding traits, due to selection for a shorter interval from weaning to estrus. Then we estimated phenotypic and genetic correlations among rearing traits, breeding traits, and rebreeding traits. Finally, we evaluated relationships involving rebreeding traits by estimating contrasts in phenotypic performance and estimated breeding values for rearing and breeding traits between sows with a normal and a delayed return to estrus.

Materials and Methods

General. The data were from a selection experiment with Dutch Landrace pigs, in which two lines were maintained. One line was selected for shorter intervals from weaning to estrus, and selection was avoided in the other line. The experiment started with a foundation population of purchased animals (generation 0), followed by seven generations of intense selection (generation 1 to 7) and one generation of relaxed selection (generation 8). Selection and management procedures were described by Ten Napel et al. (1995a).

Traits recorded from birth to entering the mating pen were weight at birth (within 24 h after birth), weaning age and weight, age and weight at moving from the nursing pen to the rearing pen, age and weight at moving from the rearing pen, and age and body condition score of the gilt at moving to the mating pen. Body condition was evaluated by experienced technicians using a well-defined scale (J. Deering, *Pig Farming* magazine, April 1979, p 31) that ranged from 0 to 5 with steps of .5. A body condition score of 0 indicates that a gilt was very thin ("Pin bones very prominent; deep cavity around tail setting; loin very narrow; sharp edge on transversal spinal processes; flank very hollow; vertebrae prominent and sharp throughout length of backbone; individual ribs very apparent"), and 5 indicates a thick fat cover ("Further deposition around pin bones, tail setting, and loin almost impossible; mid lane appears as a slight hollow between rolls of fat; ribs thickly covered with fat").

Breeding traits recorded were body condition score of sows when they entered the farrowing unit, number of pigs born and born alive, number of pigs cross-fostered, number of pigs weaned, individual pig weights at birth and weaning, and body condition score of sows at weaning. Traits calculated from these measurements were number of pigs that died during lactation, loss in body condition of sows during lactation, and daily gain in litter weight during lactation. The latter was calculated by cumulating the differences between weaning weight and birth weight of weaned individual suckling pigs and dividing this sum by the lactation length. Loss of body condition of sows was calculated as body condition score at farrowing minus body condition score at weaning.

The experimental design involved a mating period of strictly 4 wk for gilts in each mating group (Ten Napel et al., 1995a). Gilts that were not seen in estrus after 3 wk in the mating period were treated with 400 IU of PMSG + 200 IU of hCG intramuscularly to obtain a sufficient number of gilts served in the mating period. In the selection line, no progeny of treated gilts were maintained for replacement, but this restriction was not applied in the control line.

Principal Component Analysis. To aid interpretation of relationships among rearing, breeding, and rebreed-

ing traits, we calculated principal components for the rearing characteristics and the breeding characteristics. Brown et al. (1973) and Young et al. (1977) described this type of analysis in more detail. In this study, principal components that explained at least 10% of the variation were analyzed as new traits. The analysis required that all variables be measured on a sow for her data to be included. Fewer sows were, therefore, included in principal component analyses than in other analyses. A total of 904 selection-line gilts and 843 control-line gilts had complete records for rearing traits, and 1,026 sows from the selection line and 945 from the control line had complete records for breeding traits. Interval from weaning to estrus was not included in the calculation of principal components.

The principal component analysis was performed using PROC PRINCOMP in the SAS statistical package (SAS, 1985).

Genetic Parameters. The general model for estimating components of variance and covariance for rearing traits was as follows: $\mathbf{Y} = \mathbf{Xb} + \mathbf{Wc} + \mathbf{Zu} + \mathbf{e}$, where $\mathbf{Y}$ is a vector of observations, $\mathbf{X}$, $\mathbf{W}$, and $\mathbf{Z}$ are known design matrices for fixed effects ($\mathbf{b}$), common environmental effects ($\mathbf{c}$), and genetic effects ($\mathbf{u}$), and $\mathbf{e}$ is a vector of residuals. For daily gain in the nursing pen, age at weaning and age at moving to the rearing pen were included as covariables, and age at moving to the rearing pen and age at moving from the rearing pen were added as covariables for daily gain in the rearing pen. Combination of generation and mating group was fitted as a fixed effect for every trait. The sow that suckled the gilt as a pig was included in the model as a common environmental effect, with $\mathrm{var}(\mathbf{c}) = \mathbf{I}\sigma_{\mathrm{c}}^2$. Gilt was included as an animal genetic effect, with $\mathrm{var}(\mathbf{u}) = \mathbf{A}\sigma_{\mathrm{u}}^2$, in which $\mathbf{A}$ is the numerator relationship matrix. The covariance structure of residuals was $\mathrm{var}(\mathbf{e}) = \mathbf{I}\sigma_{\mathrm{e}}^2$. Covariances between $\mathbf{c}$, $\mathbf{u}$, and $\mathbf{e}$ were assumed to be zero.

The general model for estimating components of variance and covariance for breeding traits was as follows: $\mathbf{Y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$, where $\mathbf{Y}$ is a vector of observations, $\mathbf{X}$ and $\mathbf{Z}$ are known design matrices for fixed effects ($\mathbf{b}$) and genetic effects ($\mathbf{u}$), and $\mathbf{e}$ is a vector of residuals. The single fixed effect was combination of generation and mating group. Sow was included as an animal genetic effect, with $\mathrm{var}(\mathbf{u}) = \mathbf{A}\sigma_{\mathrm{u}}^2$, in which $\mathbf{A}$ is the numerator relationship matrix. The covariance structure of residuals was $\mathrm{var}(\mathbf{e}) = \mathbf{I}\sigma_{\mathrm{e}}^2$. Covariances between $\mathbf{u}$ and $\mathbf{e}$ were assumed to be zero. Interval from weaning to estrus, which is the trait under selection, was not included in the analyses.

A derivative-free REML algorithm, as applied in the MTDFREML programs (Boldman et al., 1993), was used to estimate components of variance. Estimated breeding values were obtained from these

analyses after the convergence criterion for variance component estimation was met (10^{-9}).

From the interval from weaning to estrus, we derived three new traits. Normal interval was defined as the interval from weaning to estrus, if it was 7 d or shorter. Prolonged interval was defined as the interval from weaning to estrus, if the interval was longer than 7 d. Thus, if prolonged interval was defined, then normal interval was missing, and the reverse. The third trait, incidence of a prolonged interval, was 0 if the interval from weaning to estrus was normal, and 1 otherwise.

Components of variance for binary traits were estimated using a threshold animal model. The approach followed was described by Knuiman and Laird (1990). Covariances between a binary trait and a continuous trait could not be estimated with this method using the algorithm for a sire model, described by Janss and Foulley (1993), because convergence could not be obtained.

Data from 1,881 selection-line gilts and 1,896 control-line gilts were included in the analyses of rearing traits. Numbers of sows that were included in the analyses of breeding traits were 1,165 and 1,077 for the selection and control lines, respectively.

Phenotypic Trends. Phenotypic least squares means of the traits measured were estimated with the REML procedure in Genstat (Genstat 5 Committee, 1993), using a model including line-generation and mating group within line-generation as fixed effects.

Genetic Trends. Genetic trend was obtained by regressing estimated breeding values of sows on generation number. If a is the intercept and b is the coefficient of regression of estimated breeding values on generation numbers, then

$$\begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} \mathbf{x}_1'\mathbf{x}_1 & \mathbf{x}_1'\mathbf{x}_2 \\ \mathbf{x}_2'\mathbf{x}_1 & \mathbf{x}_2'\mathbf{x}_2 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_1' \\ \mathbf{x}_2' \end{bmatrix} \hat{\mathbf{u}}$$

[1]

where $\mathbf{x}_1$ is a vector with ones for sows with a record for the trait analyzed and zero otherwise ($\mathbf{x}_1'\mathbf{x}_1$ is the total number of observations), and $\mathbf{x}_2$ is a vector with the generation number for a sow with a measurement and zero otherwise. Estimation of the standard error of b is not straightforward, because variances of estimated breeding values differ, and covariances between estimated breeding values exist. We rewrote the estimation of b so that it is a linear contrast of estimated breeding values $\mathbf{k}'\hat{\mathbf{u}}$ with

$$V(\mathbf{k}'\hat{\mathbf{u}}) = \mathbf{k}'\mathbf{A}\sigma_u^2\mathbf{k} - \mathbf{k}'\mathbf{C}^{22}\mathbf{k}$$

[2]

where $\mathbf{C}^{22}$ is the animal by animal part of the inverse coefficient matrix from the mixed-model equations used to estimate breeding values and $\mathbf{A}$ is the numerator relationship matrix. We wrote k as

$$\begin{bmatrix} \mathbf{k}'\hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_1'\mathbf{x}_1 & \mathbf{x}_1'\mathbf{x}_2 \\ \mathbf{x}_2'\mathbf{x}_1 & \mathbf{x}_2'\mathbf{x}_2 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_1' \\ \mathbf{x}_2' \end{bmatrix} \hat{\mathbf{u}}$$

[3]

Environmental Trends. Environmental trend was estimated by regressing solutions for generation-mating group effects on generation number, weighted by the number of sows with an observation in the subclass of generation and mating group, again written as a linear contrast $\mathbf{k}'\beta_i$, with variance

$$V(\mathbf{k}'\hat{\beta}_i) = \mathbf{k}'\mathbf{C}^{11i}\mathbf{k}$$

[4]

where $\mathbf{C}^{11i}$ is the generation-mating group by generation-mating group part of the inverse coefficient matrix from the mixed-model equations and k is defined by

$$\mathbf{k}'\hat{\beta}_i = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \begin{bmatrix} 0 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_3'\mathbf{W}\mathbf{x}_3 & \mathbf{x}_3'\mathbf{W}\mathbf{x}_4 \\ \mathbf{x}_4'\mathbf{W}\mathbf{x}_3 & \mathbf{x}_4'\mathbf{W}\mathbf{x}_4 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_3'\mathbf{W} \\ \mathbf{x}_4'\mathbf{W} \end{bmatrix} \beta_i$$

[5]

where $\hat{\beta}_i$ is the part of $\hat{\beta}$ that corresponds to the solutions for the generation-mating group effects; $\mathbf{x}_3$ is a vector of ones; $\mathbf{x}_4$ is a vector of generation numbers assigned to the subclass of generation and mating group; and $\mathbf{W}$ is a matrix with the number of animals with an observation per subclass on the diagonal, and zero otherwise.

Phenotypic Contrasts. Phenotypic contrasts for the principal components were estimated using PROC GLM by fitting a fixed effect indicating whether the interval from weaning to estrus was normal (0) or prolonged (1).

Genetic Contrasts. Differences in estimated breeding values for rearing traits and principal components between sows with a normal and a prolonged interval were estimated as linear contrasts of estimated breeding values $\mathbf{k}'\hat{\mathbf{u}}$ with variance equal to [2]; and k is defined by

$$\mathbf{k}'\hat{\mathbf{u}} = \begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} \bar{u}_n \\ \bar{u}_p \end{bmatrix} = \begin{bmatrix} -1 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{x}_n'\mathbf{x}_n & \mathbf{0} \\ \mathbf{0} & \mathbf{x}_p'\mathbf{x}_p \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{x}_n' \\ \mathbf{x}_p' \end{bmatrix} \hat{\mathbf{u}}$$

[6]

where $\mathbf{x}_p$ is a vector with elements equal to 0 if the interval from weaning to estrus was 7 d or shorter and 1 if the interval was longer than 7 d, and $\mathbf{x}_n$ is a vector with elements equal to 1 if the interval from weaning to estrus was 7 d or shorter and 0 if the interval was longer than 7 d. In fact, $\mathbf{x}_p$ indicates whether the observed interval was a prolonged interval and $\mathbf{x}_n$ whether the interval was a normal interval. If an animal did not have an observed interval, corresponding elements in $\mathbf{x}_p$ and $\mathbf{x}_n$ were zero.

Results

Principal Components. The major principal components obtained for the traits measured between birth and mating are presented in Table 1. The coefficients

Table 1. Eigenvectors used to calculate major principal components for rearing
traits (PC-R 1 to PC-R 4)

Trait	PC-R 1	PC-R 2	PC-R 3	PC-R 4
Birth weight	.272	−.167	−.152	.486
Weight at weaning	.396	−.247	.035	.321
Average daily gain in nursing pen	.387	−.050	.491	.062
Age at start of rearing period	−.254	.536	.220	−.099
Weight at start of rearing period	.294	.327	.610	.001
Average daily gain in rearing pen	.388	.202	−.375	−.372
Age at end of rearing period	−.318	.422	−.096	.424
Weight at end of rearing period	.324	.422	−.362	.090
Age at moving to mating pen	.058	.218	.046	.551
Body condition score at moving to mating pen	.328	.305	−.175	−.130

of the first principal component (**PC-R 1**) were similar in magnitude. The weight and gain traits had a positive sign, and the age traits had a negative sign. This principal component can be interpreted as a measure of consistent above-average growth ability. This component creates a contrast between gilts that gained above-average and were heavy at a young age and gilts that had a below-average weight at a fairly old age.

The second principal component (**PC-R 2**) had high coefficients for age traits and for weight and gain traits after moving to the rearing pen and a negative coefficient for weaning weight. Gilts with a large value for this component had above-average weight and gain records, because they were weighed at a relatively old age.

A large value for the third principal component (**PC-R 3**) indicated that the gilt initially performed above average but performed below average after moving to the rearing pen. The fourth component (**PC-R 4**) contrasted gilts that were relatively heavy at birth and weaning, relatively old at moving from the rearing pen and at moving to the mating pen, and with a poor daily gain in the rearing pen with gilts that weighed below average at birth and weaning but grew above average in the rearing pen.

The first principal component for the breeding traits (**PC-B 1**) had high coefficients for measurements of litter size, litter weight, and body condition (Table 2). This component contrasted sows with a large and heavy litter at birth and weaning, a high loss of body condition during lactation, and a poor body condition at weaning with sows with a small litter at birth and weaning that had a minor loss of body condition. So, PC-B 1 can be interpreted as a general measure of sow productivity.

The second principal component (**PC-B 2**) had high positive coefficients for average pig weight at birth and weaning, daily gain in litter weight, and litter weight at weaning, and high negative weights to numbers of pigs born, born alive, and dead during lactation. It contrasted sows with a superior milk production, but a small litter, with sows with a low milk production and a large litter.

Sows with a high value for the third principal component (**PC-B 3**) had poor body condition at farrowing, above-average body condition score at weaning, and minor loss of body condition during lactation. Their litters have above-average daily gain and weight at weaning. This principal component contrasts sows with poor body condition score at

Table 2. Eigenvectors used to calculate major principal components for breeding
traits (PC-B 1 to PC-B 4)

| Trait	PC-B 1	PC-B 2	PC-B 3	PC-B 4
Body condition in farrowing pen	.039	.016	−.505	.511
Total number of pigs born	.350	−.382	.075	.119
Number of pigs born alive	.360	−.356	.088	.108
Weight of pigs at birth	.010	.370	.043	.323
Weight of litter at birth	.375	−.189	.101	.284
Number of pigs dead during lactation	−.079	−.397	−.066	.315
Number of pigs weaned	.419	.050	.096	−.245
Weight of pigs at weaning	−.071	.366	.160	.467
Weight of litter at weaning	.373	.311	.211	.089
Daily gain in litter weight	.353	.337	.218	.025
Age sow at weaning first litter	.094	−.101	.120	.075
Body condition at weaning	−.266	−.141	.357	.370
Loss of body condition	.273	.142	−.668	−.002
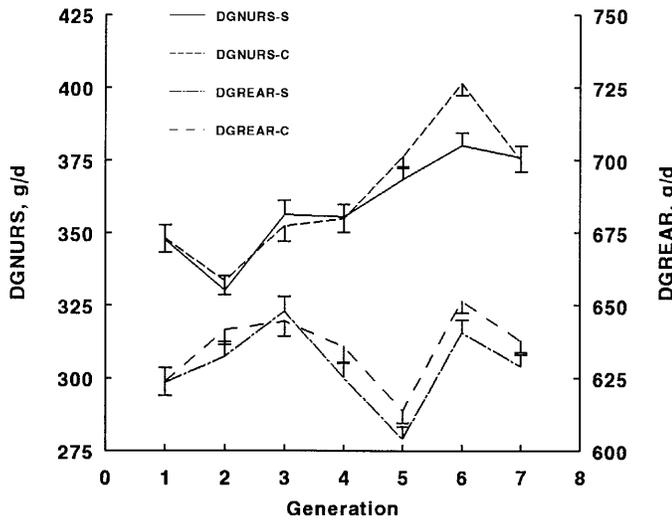
Figure 1. Average daily gain in the nursing pen (DGNURS) and in the rearing pen (DGREAR) per generation within the selection (S) and control (C) lines.

Figure 3. Number of pigs born alive (NBORNA) and number of deaths during lactation (NDEADL) per generation for the selection (S) and control (C) lines.

farrowing, a well-performing litter, and without substantial loss of body condition with sows in good condition at farrowing that suffer a large loss of body condition and have a litter that gains below average.

The fourth principal component (**PC-B 4**) can be interpreted as a measure of mothering ability. Sows with a high value for PC-B 4 were characterized by a relatively high body condition at farrowing and weaning and high pig and litter weights at birth but a high number of dead pigs during lactation and a small number of relatively heavy pigs weaned.

Phenotypic Trends. Figures 1 and 2 show development of least squares means within lines over generations for daily gain in the nursing pen, daily
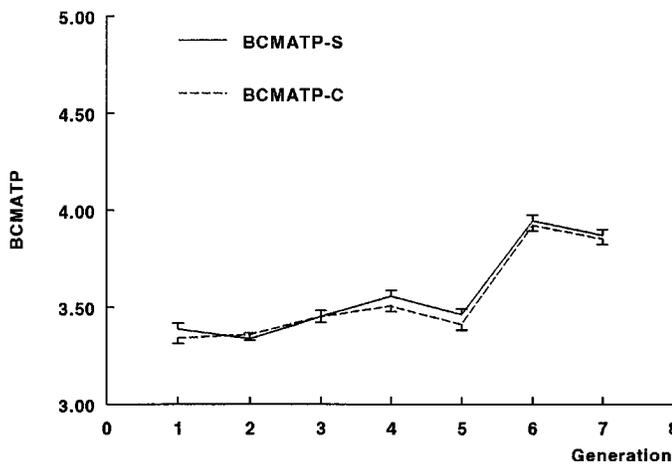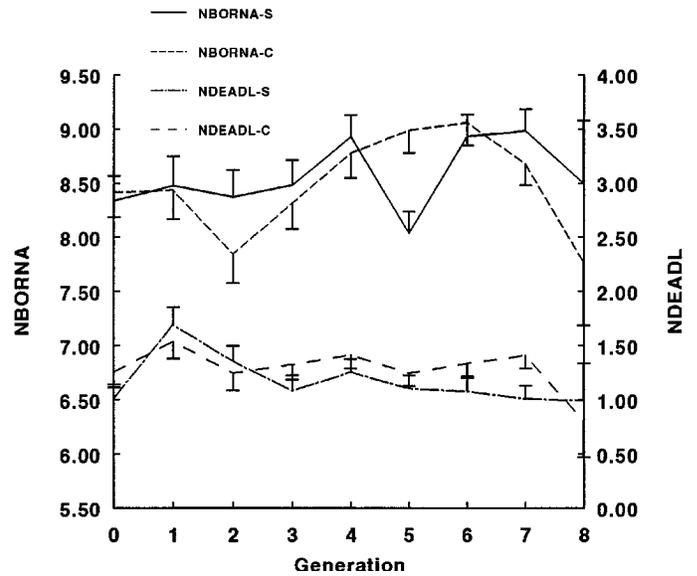
gain in the rearing pen, and body condition score upon entering the mating pen. Within-line means for these traits did not diverge during the experiment. Number of pigs born alive, number of pigs dead during lactation (Figure 3), body condition score at farrowing and weaning (Figure 4), and daily gain in litter weight (Figure 5) did not show diverging phenotypic trends due to the selection applied, either.

Genetic Parameters. Heritabilities and proportion of variance due to common environment for rearing traits, and genetic and phenotypic correlations among

Figure 2. Body condition score upon entering the mating pen (BCMATP) per generation within the selection (S) and control (C) lines.
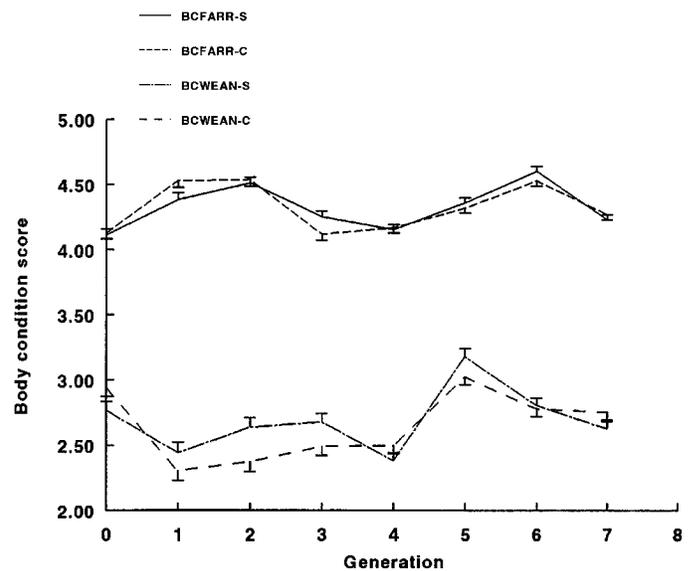

Figure 4. Body condition score at farrowing (BCFARR) and weaning (BCWEAN) per generation for the selection (S) and control (C) lines.
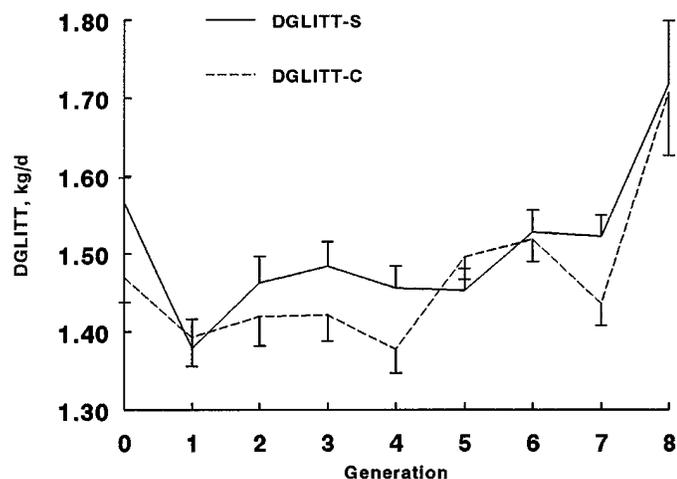
Figure 5. Average daily gain of entire litter (DGLITT) per generation for the selection (S) and control (C) lines.

these traits, are presented in Table 3. Genetic correlations among the rearing traits were moderate to high. Proportion of variance due to common environment was lower when the time between weaning and measuring the trait was longer.

Estimated heritabilities for breeding traits were low to moderate and were highest for body condition traits (Table 4). High genetic correlations were found between body condition loss and daily gain in litter weight, between pigs born alive and pigs dead during lactation, and between body condition loss and pigs born and born alive. Other high genetic correlations (number born with number born alive; body condition at weaning with body condition loss; body condition at farrowing with body condition at weaning) were high because of autocorrelation.

Heritabilities of normal intervals, prolonged intervals, and incidence of prolonged intervals (Table 5) were all lower than the heritability of the interval from weaning to estrus (.36) reported by Ten Napel et al. (1995a). The genetic correlation between normal intervals and prolonged intervals was estimated at −.04. Because normal interval and prolonged interval cannot both be observed on a sow, the residual correlation was held constant at zero.

Heritabilities of principal components of rearing traits were moderate to low (Table 5). Heritabilities of major principal components of breeding traits were moderate (Table 5).

Genetic correlations of normal intervals and prolonged intervals with daily gain in the rearing pen, body condition score in the mating pen, PC-R 1, and PC-R 3 had different signs (Table 6). Genetic correlations between breeding traits and interval from weaning to estrus were moderate to low (Table 6). Number of pigs that died during lactation had a positive genetic correlation, and body condition at farrowing and loss of body condition had negative genetic correlations with interval from weaning to estrus. The sign of the latter genetic correlation indicates that a genetic reduction of loss of body condition is accompanied by an increased interval from weaning to estrus. Genetic correlations with normal intervals had a sign different from those with prolonged intervals for body condition score at farrowing, daily gain in litter weight, loss of body condition, body condition score at weaning, and each of the four principal components. Phenotypic correlations were generally much lower than genetic correlations.

Genetic and Environmental Trends. No significant genetic trend was observed for any of the rearing or breeding traits or any of the principal components. Environmental trends were observed for daily gain in the rearing pen ($+8.8$ $g \cdot d^{-1} \cdot yr^{-1}$), body condition score at moving to the mating pen ($+.05$ units/yr), body condition at farrowing ($-.02$ units/yr), loss of body condition during lactation ($-.04$ units/yr), number of pigs born alive ($+.05$ $pigs \cdot litter^{-1} \cdot yr^{-1}$), and daily gain in litter weight ($+13$ $g \cdot d^{-1} \cdot yr^{-1}$).

Phenotypic Contrasts. Table 7 shows that gilts that had a prolonged interval to estrus after weaning their first litter and gilts with a normal interval had on average different values for PC-R 1 and PC-R 3. Gilts with a normal interval had a better overall growth ability than gilts with a prolonged interval. Poor performance in the rearing pen after initially good growth in the nursing pen increased the probability of a prolonged interval. Sows with a prolonged interval from weaning to estrus differed most from sows with a

Table 3. Heritabilities (h^2), proportion of variance due to common environment (c^2), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) among rearing traits

Trait	h^2	c^2	DGNURS	DGREAR	BCMATP
Average daily gain in nursing pen (DGNURS)	.18	.25	—	.32	.52
Average daily gain in rearing pen (DGREAR)	.24	.11	.03	—	.55
Body condition score in mating pen (BCMATP)	.37	.04	.18	.45	—

Table 4. Heritabilities (h²), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) among breeding traits

Trait[a]	h^2	BCFARP	NBORNT	NBORNA	NDEADL	DGLITT	BCLOSS	BCWEAN
BCFARP	.31	—	.17	.29	.07	.18	.07	.64
NBORNT	.11	.07	—	.97	.30	.42	.39	−.15
NBORNA	.26	.09	.92	—	.44	.46	.37	−.06
NDEADL	.09	.01	.29	.26	—	.03	−.01	.01
DGLITT	.21	.05	.21	.27	−.45	—	.58	−.25
BCLOSS	.18	.36	.24	.25	−.16	.41	—	−.73
BCWEAN	.33	.35	−.18	−.18	.17	−.37	−.75	—

[a]BCFARP = body condition score upon entering farrowing pen; NBORNT = total number of pigs born; NBORNA = number of pigs born alive; NDEADL = number of pigs that died during lactation; DGLITT = daily gain in litter weight during lactation; BCWEAN = body condition score at weaning; BCLOSS = loss of body condition during lactation; INTWE = interval from weaning to estrus.

normal interval for PC-B 1 (Table 7). Productive sows had a higher liability for a prolonged interval than other sows. Sows with a prolonged interval were also different with respect to PC-B 2 and PC-B 4. Good milk production (high daily gain in litter weight) and good mothering ability (very few pigs dead during lactation, high number weaned) increased the liability for a prolonged interval.

Genetic Contrasts. A difference in average estimated breeding values between sows with a normal and sows with a prolonged interval from weaning to estrus was found in the selection line for body condition score upon entering the mating pen, albeit this was small compared to the unit of scoring, and in the control line for PC-B 1 (Table 8).

Average estimated breeding value of sows with prolonged intervals from weaning to estrus differed from that of sows with normal intervals for number of pigs born, number of pigs born alive, daily gain in litter weight, loss of body condition, and body condition at weaning in the selection line (Table 8). In the control line, the two groups of sows had different average estimated breeding values for body condition at farrowing, daily gain in litter weight, and body condition at weaning. Figure 6 shows the contrasts in

Table 5. Proportion of variance due to common environmental effects (c²) and heritabilities (h²) of principal components for rearing traits (PC-R 1 to PC-R 4), breeding traits (PC-B 1 to PC-B 4), and interval traits

Trait	c^2	h^2
PC-R 1	.22	.31
PC-R 2	.36	.12
PC-R 3	.30	.02
PC-R 4	.41	.25
PC-B 1	—	.21
PC-B 2	—	.11
PC-B 3	—	.13
PC-B 4	—	.30
Normal intervals, d	—	.18
Prolonged intervals, d	—	.17
Incidence of prolonged intervals	—	.27

estimated breeding values per generation for each line for daily gain in litter weight and loss of body condition. The contrasts were not constant throughout the experiment but varied across lines and generations.

Discussion

None of the rearing or breeding traits studied showed a detectable trend as a correlated response to selection for shorter intervals from weaning to estrus. Principal component analysis is helpful for the interpretation of relationships between groups of traits, in this case rearing, breeding, and rebreeding traits. It combines a large number of correlated traits into a smaller number of phenotypically uncorrelated linear combinations of the traits measured. These linear combinations are not necessarily genetically uncorrelated.

The principal component analysis showed a phenotypic relationship between rearing performance and rebreeding performance, but this relationship was mainly environmental. It was only for PC-R 1 that a difference in average estimated breeding values between sows with normal and prolonged intervals was found.

A highly positive genetic correlation was found between PC-R 3 and length of prolonged intervals. Although information is lacking, it may be that the main reason for severely prolonged intervals (> 50 d) is the occurrence of cystic ovaries. A possible explanation is the following. Gilts with a high value for PC-R 3 performed well in the nursing pen, but after mixing into new groups their growth rate was below average. Mixing is a considerable stressor, so among the gilts with a high value for PC-R 3 may be gilts with a high physiological response to stressors, such as chronically elevated levels of corticosteroids, which reduces weight gain (Broom and Johnson, 1993). If these gilts respond to the stressor of weekly moving to a new pen after weaning in the same way, they may be more liable to develop cystic ovaries (Ryan and Raeside,

Table 6. Genetic (r_g), and phenotypic correlations (r_p) between rearing and breeding traits and interval from weaning to estrus, normal intervals, and prolonged intervals

	Interval weaning to estrus		Normal intervals		Prolonged intervals	
	r_g	r_p	r_g	r_p	r_g	r_p
Average daily gain in nursing pen, g/d	.19	.03	.20	.05	.25	.05
Average daily gain in rearing pen, g/d	−.24	−.11	.08	−.03	−.27	−.11
Body condition mating pen, 0–5	−.20	−.05	.15	.04	−.22	−.08
PC-R 1	−.17	−.08	.18	.03	−.27	−.07
PC-R 2	.14	−.01	.02	−.02	−.01	−.01
PC-R 3	.64	.09	−.07	.02	.62	.10
PC-R 4	−.32	.01	−.15	.01	−.52	.01
Body condition at entering farrowing pen, 0–5	−.20	−.08	.47	.05	−.26	−.06
Total no. of pigs born	.10	.08	.29	.06	.10	.06
No. pigs born alive	.14	.09	.27	.07	.15	.07
No. pigs dead during lactation	.31	−.01	.34	−.09	.44	.03
Daily gain in litter weight, g/d	−.03	.10	.34	.11	−.19	.01
Loss of body condition during lactation	−.24	.08	.49	.09	−.32	.01
Body condition score at weaning, 0–5	.04	−.14	−.09	−.06	.08	−.05
PC-B 1	.05	.13	.34	.11	−.04	.06
PC-B 2	−.24	−.01	.09	.05	−.39	−.07
PC-B 3	.37	.03	−.39	−.03	.36	.03
PC-B 4	.00	−.07	.43	−.03	−.10	−.05

1991a,b), than other sows. Hennessy et al. (1988) showed that differences in adrenal response to ACTH challenge among individual pigs were large and repeatable.

The results of this analysis confirmed that a sow's performance during lactation, and even earlier, affects the liability for a prolonged interval (reviewed by Ten Napel et al., 1995b). Productive sows (PC-B 1) were more likely to have a delayed estrus after weaning, both phenotypically and genetically. The relationship between rebreeding performance and PC-B 2 and PC-B 4 was mainly environmental.

When genetic relationships between two traits are studied in a set of data from a population selected for a third trait, then the third trait should be included in the analyses to get unbiased estimates (Pollak et al., 1984). In this case, we did not know how to include the trait under selection in the analysis properly, so we decided not to include a third trait in the analysis when estimating genetic parameters.

In a review (Ten Napel et al., 1995b), we concluded that several conditions, such as a severely catabolic state, a severe loss of body tissue, and peri- or postweaning stress, may cause a delayed estrus after weaning. It is likely that in a given population and environment more than one of these conditions contribute to the occurrence of prolonged intervals. This situation causes underestimation of genetic contrasts between sows with a normal and sows with a prolonged interval, genetic trends as correlated responses of selection for a short interval from weaning to estrus, and genetic correlations with incidence of a prolonged interval. When relationships between interval from weaning to estrus and a characteristic causing prolonged intervals are studied, prolonged intervals exist that were not due to the particular characteristic. The relationships are more severely underestimated if the percentage of prolonged intervals caused by the characteristic is low (there are many prolonged intervals due to other conditions).

If selection is against prolonged intervals, then the selection pressure is spread out over the various characteristics (e.g., stress, catabolic state, loss of body protein or fat, and high milk production) causing prolonged intervals. If the reduction in prolonged intervals is only small, the change in the various traits causing prolonged intervals may become undetectable. Furthermore, what percentage of prolonged intervals is caused by what characteristic depends on the population and the environment. So, the change in any of these characteristics depends on this percentage; if it is low, then selection pressure will be minimal. Therefore, the correlated response in these characteristics due to selection against prolonged intervals can only be expected to be linear if the environment was strictly standardized across generations, which was not the case in the current selection experiment (Ten Napel et al., 1995a).

The consequence of the above is that correlated responses in incidence of prolonged intervals due to

Table 7. Percentage of variation explained and difference between sows with normal and sows with prolonged intervals, divided by the standard deviation of the principal component

Trait	% Variation	Prolonged − normal
PC-R 1	28.1	−.128[a]
PC-R 2	17.1	−.038
PC-R 3	14.0	.095[a]
PC-R 4	11.1	.073
PC-B 1	32.4	.310[b]
PC-B 2	21.0	.129[a]
PC-B 3	10.4	−.043
PC-B 4	10.2	−.142[a]

[a]Different from zero ($P < .05$).
[b]Different from zero ($P < .001$).

selection for a particular trait cannot be predicted from the correlated response in this particular trait due to selection against prolonged intervals. Only relationships estimated in populations selected for this particular trait will be informative.

This is the main reason why this study does not confirm the results of Ten Napel and Johnson (1997), who found that average estimated breeding values for test traits were different between sows with a normal interval from weaning to farrowing and sows with a prolonged interval from weaning to farrowing. If a genetic relationship exists, it is more likely to estimate a significant genetic relationship between average daily gain or backfat depth and incidence of a prolonged interval in a population selected for daily

gain and(or) backfat than in a population selected for a short interval from weaning to estrus. Further, the two populations originated from different breeds and were managed in a different way, which may have caused differences in incidence or causes of a prolonged interval.

The differences in average estimated breeding values between sows with a normal interval and sows with a prolonged interval are evidence that selection for sow productivity may increase the genetic liability for a prolonged interval. In fact, this was observed in a selection experiment on 21-d litter weight and litter size, in which an increased interval from weaning to estrus was observed (Shurson and Irvin, 1992).

One might expect that if a trait causes prolonged intervals above a certain threshold, then a more severe state of this trait causes a more severely prolonged interval. This does not seem to hold for the traits associated with metabolic loss, except for body condition score at farrowing. Daily gain in litter weight (as a measure of milk production) and loss of body condition have a negative genetic correlation with the length of the prolonged interval. Sows with a severe loss of body tissue should be able to recover in 6 or 7 wk, when provided with an adequate diet, and resume cyclic activity soon after recovery. Prolonged intervals that are much longer are likely to have a different cause (e.g., cystic ovaries, because this condition may cause severely prolonged intervals, and it is presumably unrelated to metabolic balance). Sows with severely prolonged intervals were intermediate for daily gain in litter weight or loss of body condition, which probably caused a correlation with a different sign.

Table 8. Differences in estimated breeding values for breeding traits between sows with normal intervals and sows with prolonged intervals within lines

Trait	Selection	Control
Average daily gain in nursing pen, g/d	1.17	−.91
Average daily gain in rearing pen, g/d	−1.34	−1.35
Body condition score at entering mating pen, 0–5	−.033	−.018
PC-R 1	−.023	−.103[b]
PC-R 2	−.018	−.020
PC-R 3	.002	.003
PC-R 4	.025	.002
Body condition score at entering farrowing pen, 0–5	−.022	−.031[b]
Total no. of pigs born	.108[b]	.039
No. pigs born alive	.066[b]	.024
No. pigs dead during lactation	.001	−.011
Daily gain in litter weight, g/d	26.7[c]	14.0[b]
Loss of body condition during lactation	.035[b]	.012
Body condition score at weaning, 0–5	−.071[c]	−.055[c]
PC-B 1	.190[c]	.082[a]
PC-B 2	.008	.017
PC-B 3	.011	.011
PC-B 4	.014	−.057[a]

[a]Different from zero ($P < .10$).
[b]Different from zero ($P < .05$).
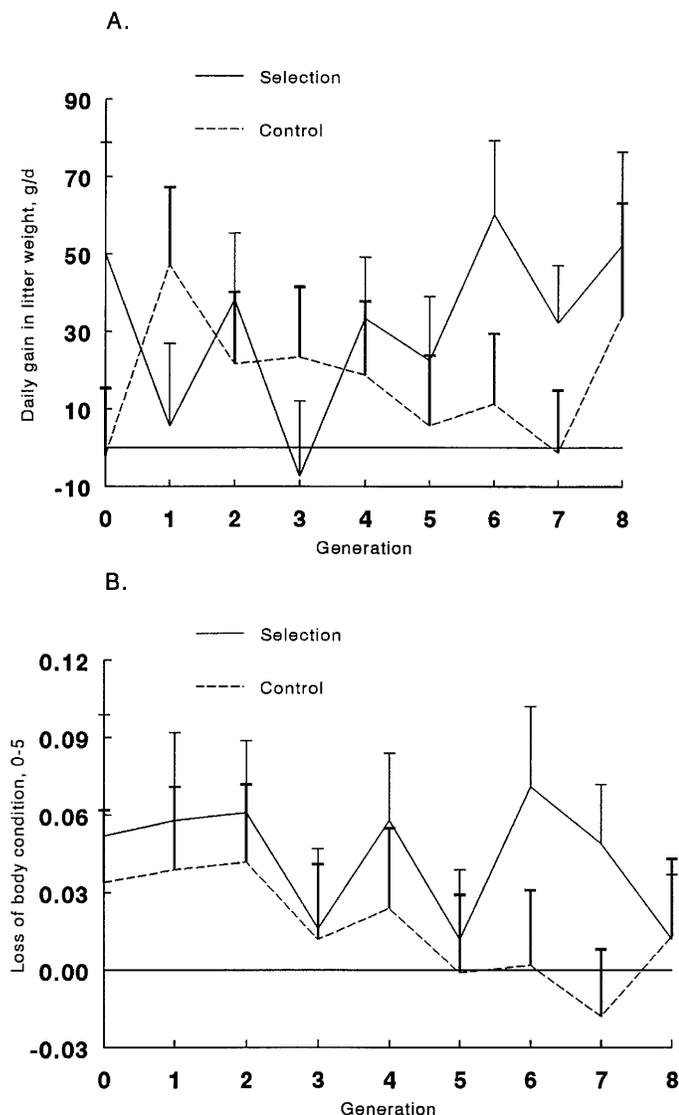[c]Different from zero ($P < .01$).

A.

B.

Figure 6. Development of differences in estimated breeding value between sows with a normal interval and sows with a prolonged interval within lines across generations for average daily gain in litter weight (A) and loss of body condition (B).

Splitting a sorted set of observations on a trait into two groups and analyzing the selected groups separately yields estimates for heritabilities and correlations that deviate from the estimates from the original set. Such an analysis is difficult to interpret in general, because a selected set of observations is omitted from the analysis. For normal and prolonged intervals, however, the situation is different, because we consider them as separate traits measured on the same scale. The difference between traits is whether problems delay onset of cyclic activity. The distinction is supported by the estimate of the genetic correlation between normal and prolonged intervals, which is essentially zero.

Genetic analysis of the interval from weaning to estrus may not be proper if it is not taken into account

whether the interval was normal or prolonged, because normal and prolonged intervals are regressed to a common mean that is dependent on the incidence of prolonged intervals. This makes it difficult to compare the estimate of the heritability of the interval from weaning to estrus with those of the three components. Also, genetic correlations with interval from weaning to estrus, interval from weaning to farrowing, or farrowing interval may not be useful for predicting a correlated response in these traits.

In conclusion, genetic selection for a short interval from weaning to estrus did not cause a measurable change in any of the rearing or breeding traits studied. We have argued, however, that the reverse does not hold; genetic selection for some of these traits may change the genetic liability for a prolonged interval as a correlated response.

Implications

Correlated responses to selection for a short interval from weaning to estrus are small and depend highly on the environment in which the population is selected. Selection for rearing and breeding traits, however, may cause a correlated response in incidence of prolonged intervals. Genetic relationships between any trait and rebreeding performance should be studied taking into account that intervals from weaning to estrus consist of normal intervals and prolonged intervals.

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